

## PROMPT PUBLICATION

The author can greatly assist the Publishers of this Journal in attaining prompt publication of his paper by following these four suggestions:

1. *Abstract.* Send with the manuscript an Abstract containing not more than 250 words, in the precise form of The Bibliographic Service Card, so that the paper when accepted can be scheduled for a definite issue as soon as received by the Publisher from the Editor.

2. *Manuscript.* Send the Manuscript to the Editor prepared as described in the Notice to Contributors, to conform to the style of the Journal (see third page of cover).

3. *Illustrations.* Send the Illustrations in complete and finished form for engraving, drawings and photographs being protected from bending or breaking when shipped by mail or express.

4. *Proofs.* Send the Publisher early notice of any change in your address, to obviate delay. Carefully correct and mail proofs to the Editor as soon as possible after their arrival.

By assuming and meeting these responsibilities, the author avoids loss of time, correspondence that may be required to get the Abstract, Manuscript and Illustrations in proper form, and does all in his power to obtain prompt publication.

Resumen por el autor, T. W. Todd.

Significación numérica de las vértebras torácico-lumbares de los mamíferos.

1) Las siguientes ideas aceptadas con relación a la columna vertebral presacra de los mamíferos son indudablemente correctas. El número primitivo de vertebras torácico-lumbares de los mamíferos es y ha sido siempre diecinueve. En la mayor parte de los órdenes de los mamíferos existe una tendencia a aumentar este número (grupo auxispondílico de Welcker). En los Primates la tendencia es hacia la reducción de dicho número, formando los antropoides y el hombre el grupo lipospondílico de Welcker. En los referente a la columna torácico-lumbar, el hombre ocupa un lugar entre los gibones y los antropoideos negros gigantes. 2) Los lemures forman un eslabón entre los Primates y los demás órdenes de mamíferos. Mientras que algunos de ellos exhiben en su especialización un aumento en el número, del mismo modo que los mamíferos auxispondílicos, existen otros que se aproximan a los Primates gigantes típicos en su tendencia hacia la reducción del número de las vértebras torácico-lumbares. La relación de la fórmula vertebral con la especialización de los lemures es muy significativa. 3) Los monos del Nuevo Mundo presentan una tendencia mayor hacia la reducción en número, pero aquí también existe una tendencia marcada hacia el aumento en número, como ocurre en muchos lemures. 4) El número primitivo, diecinueve, es característico de las dos subfamilias de monos antropoides del Antiguo Continente, encontrándose un aumento a veinte lo en raros casos. 5) Los antropoides y el hombre exhiben una reducción progresiva en el número de vértebras, pero en todo este grupo el hombre presenta la condición numérica más estable en su fórmula vertebral. La estabilidad precisa en el hombre está ilustrada de un modo sorprendente en el trabajo reciente de Willis.



# NUMERICAL SIGNIFICANCE IN THE THORACICOLUMBAR VERTEBRAE OF THE MAMMALIA

T. WINGATE TODD

*Anatomical Laboratory, Western Reserve University, Cleveland, Ohio*

## CONTENTS

|                                                                                                         |     |
|---------------------------------------------------------------------------------------------------------|-----|
| Introduction .....                                                                                      | 261 |
| Historical aspect of phylogenetic shortening of the presacral column in<br>Man and other Primates ..... | 265 |
| The thoracicolumbar vertebrae in lower mammals .....                                                    | 267 |
| The Primate vertebral column .....                                                                      | 271 |
| The thoracicolumbar vertebrae of the lemurs .....                                                       | 271 |
| The thoracicolumbar vertebrae in the New-World monkeys .....                                            | 277 |
| The thoracicolumbar vertebrae of the Old-World apes .....                                               | 278 |
| The thoracicolumbar vertebrae in the anthropoids .....                                                  | 280 |
| Summary .....                                                                                           | 284 |
| Literature cited .....                                                                                  | 285 |

## INTRODUCTION

In a study of the vertebral column where the question of anomalies, whether of development or of constitution, must play so prominent a rôle, it is essential that the type, or what is often called the normal, be very clearly understood. And what is equally important, the steps by which this type came into being should be investigated and made plain. Without the latter study one could have no adequate background for a correct understanding of the type. Now the area under discussion, namely, the presacral vertebral column, is defined above by the occiput with the peculiar atlas and axis vertebrae. This special arrangement of the uppermost vertebrae effectively precludes any mistake in identification of the individual bones. Even when the atlas is more or less absorbed into the occipital bone itself, there can be no doubt as to its identity. At the other end the presacral column is defined by the sacrum. Here we do not find an equally clear distinction; there may be an intermediate

form present, defined as a lumbosacral vertebra. For it is well known that the sacrum does not always lie at precisely the same level even in the same species. As the first problem is to inquire into the number of presacral vertebrae and the relation of this number to the phylogenetic position of the various Primates, it is obvious that we must first form a clear impression of the usual constitution of the bones of the presacral column and examine what tendency there may be towards stability of number.

The use of the words *type* and *normal* a little higher up was merely to introduce the reader to the subject in terms with which he is familiar. Both words are, however, frequently used very loosely and in various senses; therefore it is proposed to substitute for them the mathematical expression *mode*, which conveys merely the idea of most frequent occurrence. One would then restate the problem in the following questions: What is the modal number of presacral vertebrae in the various Primates? What stability does this number show? By what steps was it reached?

A review of the mammalian vertebral column, including that of Man, discloses clear evidence of instability of morphological constitution, especially in the cervicothoracic, thoracolumbar and lumbosacral regions. It is the last mentioned which will occupy our attention for the present, although it is impossible to make an adequate study of one area without glancing at times in the direction of the others.

The number of presacral vertebrae in Man is usually asserted to be twenty-four, and the twenty-fifth vertebra is the first sacral according to general acceptance. These statements are only an approximation of the truth: they take no account of the frequent massive variations, and, further, they appear to infer that even in details there is a uniformity which certainly does not exist. We shall make use often of the term presacral vertebrae, and therefore take this occasion to define the expression. Now, of these presacral vertebrae, certain belong to the neck. In mammals these are almost constantly seven in number, the exceptions being beyond our present discussion, although it may be stated in passing that the so-called anomalies in number of



cervical vertebrae do not constitute so marked a stumbling-block to the uniformity of the class Mammalia, or so difficult a problem in phylogeny, as some investigators would have us imagine. We may take it, then, that the number of cervical vertebrae in the mammals generally is seven. Hence, if we know the total of presacrals, we can readily ascertain the number of vertebrae comprising the thoracic and lumbar series together. Since the sole distinction between these series is the possession of the ribs by the former, and since there is marked instability in the exact morphology of the thoracolumbar junction, by which statement we mean that there may be some difficulty in ascertaining exactly at what point one series ends and the other begins, and whereas we desire above all to keep our immediate problem as free as possible from confusing complications, we shall find it convenient to avoid making a distinction between thoracic and lumbar regions and shall therefore consider the vertebrae of both together as the thoracolumbar series. From the earlier part of this paragraph it is plain that the conventional number of thoracolumbar vertebrae in Man is seventeen. Now, since we shall not introduce without specific mention into our discussion the vertebral formula of any mammal which has other than seven cervical vertebrae, we may take it that a variation in the total number of the thoracolumbar vertebrae infers a change in the position of the lower (or hind) limb relative to the vertebral column.

There is another point which must receive preliminary emphasis, namely, the sacrum. The sacrum is merely a composite bone formed by the fusion of certain vertebrae. The factors which, in the aggregate, influence this fusion lie, for the most part, beyond our present consideration. The number of vertebrae comprising the sacrum has no value for this study. The number of vertebrae belonging to and forming the part of the sacrum which articulates with the os innominatum, on the other hand, is of the most absorbing interest, and it is expected that a later communication will convey the results of this study. We consider, at the moment, not the center of articulation between vertebral column and hind limb, but the cephalic delimitation of

this articulation. When we say that the twenty-fifth vertebra is the first sacral we mean that the cephalic delimitation of the articulation with the hind limb is to be found in the twenty-fifth segment from the occiput.

Whereas the number of cervical vertebrae in mammals is commonly known to be practically constantly seven, it is not so apparent that the number of thoracic and lumbar vertebrae is remarkably constant among the Mammalia, diverse though they are in their several bodily conformations, habits, and modes of progression. The following table is taken from Gregory's suggestive memoir upon mammalian orders (7):

|                     | THORACICOLUMBAR<br>VERTEBRAE (AVERAGE) |
|---------------------|----------------------------------------|
| Monotremata .....   | 19-20                                  |
| Marsupialia .....   | 19                                     |
| Creodonta .....     | 20                                     |
| Carnivora .....     | 20                                     |
| Lemuroidea .....    | 19-20                                  |
| Rodentia .....      | 19                                     |
| Artiodactyla .....  | 19-20                                  |
| Insectivora:        |                                        |
| Tupaia .....        | 19-20                                  |
| Gymnura .....       | 20                                     |
| Microgale .....     | 22                                     |
| Solenodon .....     | 19-20                                  |
| Sorex .....         | 20                                     |
| Galeopithecus ..... | 18-19                                  |

It must be understood that this table conveys only the most general impression of the number of thoracicolumbar vertebrae in several mammalian orders. The purpose of the moment is simply to draw attention to the comparative frequency of occurrence of the number of 19-20 among mammals, and at the same time to indicate, in the Insectivora, how specialization or divergence from the stem group is associated with a number differing from that which is most frequent in occurrence and most characteristic of the class.

Just as the typical mammalian number of cervical vertebrae is seven, so the number of vertebrae in the thoracicolumbar series of the primitive mammal is either nineteen or twenty; this variation representing the usual limits of divergence. A prim-



itive mammal is one which has retained archaic features in marked degree. It is obvious that any particular mammal may be primitive in certain features, but not in others.

We may assume that nineteen is the primitive number of thoracolumbar vertebrae in the mammal and that the total primitive number of presacral vertebrae is twenty-six ( $19 + 7$ ). Therefore, the first sacral vertebrae in the primitive mammal is the twenty-seventh.

With these preliminary definitions of the primitive mammalian column clearly in mind, it is proposed to examine the vertebral formulae of the various Primates in order to ascertain, if possible, what has happened to the lower part of the presacral series during the evolution of the creature Man.

#### HISTORICAL ASPECT OF PHYLOGENETIC SHORTENING OF THE PRESACRAL COLUMN IN MAN AND OTHER PRIMATES

That there has been in Man a phylogenetic shortening of the presacral column has been recognized for a very long time. When Sir Richard Owen was Conservator at the College of Surgeons' Museum, comparison of the number of presacral vertebrae in Man and in other mammals formed one of the points of his discourses. At that time one, Holmes Coote, a demonstrator of anatomy at Saint Bartholomew's Hospital, fell under the magnetic influence of Owen, and, with the encouragement of the Master, attempted to introduce into the regular undergraduate courses in anatomy for the several examinations of the College those principles of comparative anatomy which he had absorbed in Owen's lectures. Thus it happened that in 1849 Coote published a work entitled "Homologies of the Human Skeleton," not professing to be original in any way, but merely to bring before the London students, as best he might, the views and researches of his instructor. The book is poorly written and is plainly the work of one who has enthusiastically jotted down during a lecture the fragmentary information which he gleaned in the moments which could be spared actually to listen to the words of the lecturer. The sequence of the paragraphs is disconnected; there is many a hiatus which can indeed be filled in by one who

is acquainted with what Owen was likely to say, but not by the students for whom the volume was written. At the beginning of the second chapter (1, pp. 25, 26) there is an effort to present Owen's views upon the significance of the number of thoracolumbar vertebrae. This is perfectly clear to those who know their Owen (16, especially vol. 2, pp. 493-494 and 512). Coote meant to convey the idea of significant uniformity in the total number of thoracolumbar vertebrae among the Carnivora as opposed to the double series (i.e., Artiodactyla and Perissodactyla) among ungulates; that the number, with certain clearly explicable exceptions, is twenty among the Carnivora; and that, taking the number in Carnivora as a basis, there is continuous reduction throughout the Primates until the anthropoids and Man are reached. This idea undoubtedly became very well fixed in the minds of anatomical teachers, and one of the evidences of its propagation is to be found in the attempt by Paterson (17) to prove a tendency towards elongation of the presacral column rather than towards reduction, with references to anthropoid apes and 'quadrupeds.' The conception of an evolutionary shortening of the presacral column in Primates through transmutation and not by suppression is carried on by Keith (13) in an article full of information and suggestion, published in 1902. The same idea formed the basis of the first communication of Rosenberg in 1876 (18). This, indeed, was the earliest concrete formulation of the conception generally held, and as such has rightly come in for a full share of recognition. Subsidiary additions made by Rosenberg at later dates do not carry equally convincing force.

Five years later, Welcker, disagreeing in some points with Rosenberg, differentiated between two types of mammals. The primitive presacral number of twenty-six vertebrae is retained in most mammals. Among these there is seen to be a tendency towards lengthening of the column. In marked contrast stands another type of mammal—the tailless apes and Man—in which occurs a shortening process. These Welcker termed lipospondylous, in contradistinction to the other group of auxispondylous type (19).



There is, then, nothing new in the perception of a phylogenetic shortening of the presacral column in Primates. As the introduction to a comprehensive study of the vertebral column in man upon a material of hitherto unattainable amount and completeness, of which one contribution is already in the press (20), it becomes necessary to examine this theory in detail and especially in reference to evidence of a phylogenetic nature afforded by other parts of the body.

#### THE THORACICOLUMBAR VERTEBRAE IN LOWER MAMMALS

The Monotremata are the most ancient survivals among mammals, and it is therefore important to notice their presacral formula. Gregory quotes Howes as identifying nineteen thoracicolumbar vertebrae in both genera, namely *Ornithorhynchus* and *Echidna* (except *Proëchidna* which would have twenty) (7, p. 152), and continues: "But in the view of the writer the anterior sacral is only a modified lumbar and the posterior sacral only a slightly modified caudal. In that case the vertebral formula would be as follows:

"Ornithorhynchus C.7, T.17, L. 2, S.1, CS.1, Cd.19;  
                   *Echidna*           C.7, T.16, L. 5, S.2, —, Cd.10."

In tracing down this reference I find that the citation of Howes' name is certainly a slip of the pen. The reference is really to Flower's *Osteology* (6). Now it appeared to me that the statement of Gregory might indicate some instability occurring in the lumbosacral region of these lowly and very specialized mammals, primitive though they are in many particulars. I have therefore studied closely the three skeletons in the Hamann Museum. Our *Ornithorhynchus*, B.174, shows no sign whatsoever of ambiguity in the last lumbar or first sacral vertebra. It is true that the last (third) sacral vertebra might very well be called caudal, although there are sufficient points of distinction to make clear its appropriate position. Only two sacral vertebrae take part in the articulation with the ilium. Therefore, the vertebral formula as I would state it for this example is:

C.7, T+L.19, S.2+1, Cd. —.

Our two examples of *Echidna* are both *E. aculeata*. Neither shows the least sign of ambiguity in the lumbosacral region. In both the upper three pieces of the sacrum articulate with the ilium and for both the vertebral formula is:

C.7, T+L.19, S.3+1, Cd. —.

I would make the same reservation for the last sacral in these skeletons as in the case of our *Ornithorhynchus*.

In order to enlarge the material upon which conclusions of sufficient accuracy may be drawn, I have referred to the Catalogue of the College of Surgeons (5). In this catalogue Flower cites five examples of *Ornithorhynchus* skeletons, all of which show a thoracolumbar column numbering nineteen vertebrae. In each case also the sacrum was formed of three vertebrae, though naturally it is not stated how many of these articulated with the ilium. There are four skeletons of *Echidna*, all of which possess nineteen thoracolumbar vertebrae. Two have three sacral vertebrae and two have four.

Now, in the face of these facts, one can only infer that the skeletons examined by Gregory were unusual in the conformation of the lower lumbar column and that it is certainly more correct to describe the Monotremata as possessing nineteen thoracolumbar vertebrae.

We note that this number nineteen is practically constant also for the Marsupialia, the next most ancient group of mammals.

Turning to the placental mammals, we would naturally first inquire the condition in the insectivores because of the central position of this order, and in the Rodentia which also represent a very ancient and, in many ways, relatively little changed order.

The importance of these orders in a study of other mammals was emphasized many years ago by Huxley. "Given the common plan of the Insectivora and of the Rodentia, and granting that the modifications of the structure of the limbs, of the brain, and of the alimentary and reproductive viscera which occur among them may exist and accumulate elsewhere, and the derivation of all the Eutheria from animals which, except for their simpler placentation, would be Insectivores, is a simple deduction from the law of evolution" (12, p. 657).



For a general survey of the vertebral formula there is no better reference than the Catalogue of the College of Surgeons (5), for both Owen and Flower paid attention to this matter. One has only to turn the pages of this catalogue to be impressed with the remarkable constancy of the number nineteen in the thoracicolumbar column of rodents. A certain number of very specialized genera, it is true, show a somewhat greater number, and here and there an odd individual may possess twenty in the vast majority of the genera in which nineteen thoracicolumbars are typical. This is quite what one would expect and merely serves to confirm the assertion that nineteen is the general mammalian number.

The insectivores present a rather different case. All of these are specialized, some very greatly. Yet even among insectivores the less specialized and aberrant possess the typical thoracicolumbar number. The lipotyphlous insectivores should of course be distinguished from the Menotyphla.

The total thoracicolumbar number in the insectivores is unusually unstable. For example, the number in *Gymnura*, the genus specially picked out by Huxley for its importance as a relatively undifferentiated Eutherian, has twenty according to Flower (6, p. 86), twenty according to the Catalogue (5, p. 647), but twenty-one (i.e.,  $16 + 5$ ) in our specimen B 545.

Of all existing insectivores the Tupaiidae, or Tree Shrews of the Orient, probably show most faithfully the conditions reminiscent of the stem placentals. For a full discussion of the probable ancestry of the mammals with significant details of the habits and mode of life of these, as yet largely hypothetical, creatures the reader is referred to the article by Matthew on the arboreal ancestry of the Mammalia (14). The well-established belief that *Tupaia*, besides being one of the most generalized insectivores, lies not far from the point of divergence of Primates and insectivores, renders this animal of special interest, and Gregory's remarks (7, p. 288) are particularly suggestive.

Of existing Menotyphla the skeleton of the arboreal Tupaiidae appears far more generalized, especially in the limbs and backbone, than does that of the terrestrial, saltatorial *Macroscelididae*.

There is also considerable indirect evidence for ascribing to the stem Insectivores semi-arboreal insectivorous-omnivorous habits.

Such habits seem the best fitted to give rise by adaptive radiation to all others. The habit of running along the branches, of jumping from branch to branch, favors an even development of all the muscles of the limbs, hands and feet and puts a premium on a high average development of mental faculties; whereas aquatic, fossorial, cursorial, saltatorial and volant habits all imply limitation of movement of the limbs in particular directions, and the hypertrophy of certain parts at the expense of others, with resultant one-sided specialization of the nervous system. This is fully illustrated in the various types of terrestrial, aquatic and fossorial Insectivores, which are all highly specialized in these directions; whereas the trunk and limbs of the arboreal Tupaiidae are distinguished not only by the almost entire lack of hypertrophy of one part over another but also by the retention of very numerous characters (such as a free centrale carpi, a third trochanter, entepicondylar foramen, pentadactyly, etc., etc.), which, on any theory, are admitted to be primitive mammalian characters.

The semi-arboreal habit also favors the retention of small size and it is obvious that the opposite condition, increasing size and weight, means larger muscles and greater need for the development of special processes on the bones; this tends as it were, to upset the balance of form-determining forces and to start new or peculiar lines of specialization.

Our single skeleton of *Tupaia tana*, B. 211, has the following vertebral formula:

C.7, T+L.19, S.1+2, Cd. —.

The thoracolumbar column retains the primitive number of pieces, and an equally significant fact is that the first piece of the sacrum alone articulates with the ilium, although the sacrum consists of three pieces. Thus *Tupaia* shows an articulation with the ilium more primitive in character than even the monotremes. Nineteen thoracolumbars is the number accorded by Gregory from a specimen in the National Museum, and it is the number in the College of Surgeons specimen (5, p. 649). But Gregory cites evidence of a variation in number from eighteen to twenty (7, p. 275).

The other Tree Shrew, by name *Ptilocercus*, not so lemur-like as *Tupaia*, also presents nineteen thoracolumbar vertebrae (9). On the other hand, the terrestrial Macroscelididae show the beginning of the usual mammalian tendency to increase this number. Gregory quotes de Blainville and Mivart to the effect that Macroscelides has either nineteen or twenty thoracolum-



bars (7, p. 282), and Peters as giving twenty-one to Rhynchocyon. The College of Surgeons specimen of Rhynchocyon also presents twenty-one (5, p. 649).

#### THE PRIMATE VERTEBRAL COLUMN

We pass now to consider the Primate vertebral column, bearing in mind that the stem Primates diverged from the common insectivorous-omnivorous stem placentals when the latter were in a stage of bodily formation probably not so very unlike our modern Tree Shrews. Thus in all likelihood the number of the thoracicolumbar vertebrae in the ancestral stem Primates was nineteen.

#### THE THORACICOLUMBAR VERTEBRAE OF THE LEMURS

Upon the assumption that the further back in the history of any form of animal one goes the more likely one is to discover the primitive or parent type, we glance at the paleontological story of the Primates. There is no doubt that the lemurs represent the earlier and more primitive form and that in many respects the New-World monkeys retain lemur-like features.

The Old-World Primates higher than the lemurs are structurally much further removed from the lemurs. The Old-World apes differ in many respects from the anthropoids and Man, so that it is better to keep them separate in mind, merely with the small anthropoid *Hylobates*, the Gibbon, as a connecting link.

Now the lemuroid characters of *Tupaia* may be due to convergent evolution, but, as Gregory says, "the provisional conclusion is that the *Tupaia*idae are descended from the Insectivore stock that gave rise to the Primates" (8). We are to examine the Primate history therefore with the features of *Tupaia* in mind, recalling especially the primitive number of thoracicolumbar vertebrae.

The most ancient lemur known is the Eocene form *Notharetus*, the skeleton of which is considerably more primitive than that of any later Primate (Gregory, 10). Unfortunately, the complete vertebral column is not known, but the skeleton so closely resembles that of modern lemurs in principle, though not in proportions, that we may feel confident in attributing to *Notharetus*

the same number of thoracolumbar vertebrae as in existing species. After all, this is really the important feature of the search for an ancestral form; the modern species have probably not traveled far in their skeletal pattern from their progenitor. As in Lemur, the articular surface for the ilium is borne almost entirely by the first sacral vertebra (Gregory, 11). This is also evidence of the probable identity of the vertebral formula of *Notharctus* with that of *Lemur*. Some lemurs retain a greater number of primitive characters than others; some lemurs are very specialized and aberrant. Therefore, it will not do for us to take an average over the thoracolumbar columns of many individual specimens; our specimens must be arranged. For this reason, among others, the well-known work of Le Double has been of singularly little service to me. Indeed, I am strongly of the opinion that it is actually misleading unless used with precaution. I have extracted the records of vertebral formulae from the Catalogue of the Royal College of Surgeons (5) and added these to our own records here with the following results.

There is nothing more distressing and time-consuming than the attempt to identify exact species and sometimes even genera of Primates from the data given by most authors. This confusion has grown up more in reference to the brain than in other morphological fields. But even in the skeleton it is not wanting. In order to avoid possible misunderstanding, I have named all the specimens in the following pages in accordance with D. G. Elliot's monograph, which in spite of certain shortcomings is the most generally useful standard for reference (2).

*Lemurinae*

*Lemur*:

|                                   |        |         |         |
|-----------------------------------|--------|---------|---------|
| <i>L. catta</i> Linnaeus.         | T+L 20 | W.R.U., | B. 137. |
| <i>L. catta</i> Linnaeus.         | T+L 19 | W.R.U., | B. 197. |
| <i>L. catta</i> Linnaeus.         | T+L 18 | R.C.S.  | 265.    |
| <i>L. variegatus</i> Kerr.        | T+L 19 | W.R.U., | B. 344. |
| <i>L. variegatus</i> Kerr.        | T+L 19 | R.C.S., | 262.    |
| <i>L. albifrons</i> ? E Geoffroy. | T+L 19 | R.C.S., | 270.    |
| <i>L. mongoz</i> ? Linnaeus.      | T+L 19 | R.C.S., | 271.    |
| <i>L. mongoz</i> ? Linnaeus.      | T+L 19 | R.C.S., | 272.    |
| <i>L. sp.</i>                     | T+L 19 | W.R.U., | B. 138. |

*Lepidolemur*:

|                                    |        |         |         |
|------------------------------------|--------|---------|---------|
| <i>L. ruficaudatus</i> Grandidier. | T+L 21 | W.R.U., | B. 345. |
|------------------------------------|--------|---------|---------|



*Chirogaleinae*

|                         |        |         |         |
|-------------------------|--------|---------|---------|
| Microcebus:             |        |         |         |
| M. murinus Miller.      | T+L 20 | W.R.U., | B. 434. |
| M. murinus Miller.      | T+L 20 | R.C.S., | 281.    |
| M. fureifer Blainville. | T+L 20 | R.C.S., | 279.    |
| Myoxicebus:             |        |         |         |
| M. griseus E. Geoffroy. | T+L 18 | R.C.S., | 260.    |

*Indrisinae*

|                     |        |         |         |
|---------------------|--------|---------|---------|
| Propithecus:        |        |         |         |
| P. diadema Bennett. | T+L 20 | R.C.S., | 255.    |
| Indris:             |        |         |         |
| I. indris Gmelin.   | T+L 21 | W.R.U., | B. 343. |
| I. indris Gmelin.   | T+L 21 | R.C.S., | 252.    |
| Lichanotus:         |        |         |         |
| L. laniger Gmelin.  | T+L 21 | R.C.S., | 258.    |

*Daubentonidae*

|                             |        |         |         |
|-----------------------------|--------|---------|---------|
| Daubentonia:                |        |         |         |
| D. madagascariensis Gmelin. | T+L 19 | W.R.U., | B. 198. |

*Lorisinae*

|                           |        |         |         |
|---------------------------|--------|---------|---------|
| Perodicticus:             |        |         |         |
| P. potto E. Geoffroy.     | T+L 21 | R.C.S., | 294.    |
| Arctocebus:               |        |         |         |
| A. calabarensis Smith.    | T+L 22 | R.C.S., | 297.    |
| Loris:                    |        |         |         |
| L. tardigradus Linnaeus.  | T+L 23 | R.C.S., | 288.    |
| L. tardigradus Linnaeus.  | T+L 23 | R.C.S., | 289.    |
| L. tardigradus Linnaeus.  | T+L 23 | R.C.S., | 291.    |
| Nycticebus:               |        |         |         |
| N. borneanus Lyon.        | T+L 23 | W.R.U., | B. 136. |
| N. javanicus E. Geoffroy. | T+L 23 | R.C.S., | 292.    |

*Galaginae*

|                                |        |         |      |
|--------------------------------|--------|---------|------|
| Galago:                        |        |         |      |
| G. crassicaudatus E. Geoffroy. | T+L 19 | R.C.S., | 283. |
| G. alleni Waterhouse.          | T+L 19 | R.C.S., | 287. |

*Tarsiidae*

|                      |        |         |         |
|----------------------|--------|---------|---------|
| Tarsius:             |        |         |         |
| T. borneanus Elliot. | T+L 19 | W.R.U., | B. 135. |

Although the combined series of lemurs here presented is not large, it is comprehensive enough to be exceedingly suggestive. The frequent recurrence of nineteen thoracicolumbar vertebrae cannot be without significance, especially when one recalls that this number is characteristic of all primitive mammals. Our

knowledge of the history and the relationships of the lemurs makes us accept unhesitatingly the inference that the number nineteen is equally indicative of a primitive character in these animals. But there are numerous deviations from the number nineteen, and these with two exceptions are in the direction of a higher number. We have seen the same tendency in insectivores and it is duplicated in other mammalian orders. The Perissodactyla, for example, have all deviated in the direction of a longer thoracolumbar column. That the number increases, and that the increase should be within strict limits, indicates the phylogenetic or evolutionary trend. That a similar increase should be found among many varied types of mammal is what we should expect from the general principles of parallel evolution. Now, if we simply say that among twenty-nine lemurs the number of thoracolumbar vertebrae is nineteen in 11 cases, eighteen in 2, twenty in 5, twenty-one in 5, twenty-two in 1, and twenty-three in 5, we shall fail altogether to grasp the real significance of the variation. In order to appreciate properly the trend of the variation, we must examine the relationships of these genera and species to each other.

To define adequately the degree of affinity of one animal to another is no easy matter, for it is naturally purely relative, and about the precise position there may be some reasonable difference of opinion. Nevertheless, the marshalling of these lemurs may be attempted in a general way. We shall take as our guide, in the first place, the characters of the lemur brain as set forth by Elliot Smith (4), and, secondly, certain unpublished notes made by myself upon the skull and teeth of the lemurs for a forthcoming work.

Now, of all the lemurs *Tarsius* is undoubtedly the most primitive, although not far from it in primitive characters come the galagos. Closely related to the galagos, but more specialized are the pottos (*Perodicticus*), and still more specialized are the genera *Loris* and *Nycticebus*, which are intimately related one to another, frequently confused in description, and imperfectly separated zoologically. If, now, the table of vertebrae be consulted with the foregoing general statement in mind, the wonder-

fully accurate manner in which the increase in length of the thoracolumbar column keeps pace with the general evolutionary trend appears most striking. The number nineteen in *Tarsius* and the galagos gives place to twenty-one and two in the pottos and to twenty-three in *Loris* and *Nycticebus*. I am aware that I am not giving in detail the arguments of Elliot Smith on the brain or my own on skull and dentition. The former can be obtained from the original paper (4) and the latter will be available later. But it is rather striking that work carried out upon parts of the body so distinct as brain on the one hand and teeth and skull on the other gives such harmonious results.

As to the genus *Lemur* itself, there is very little comment to make. All the species are much alike in their anatomical features. They are less primitive than *Tarsius* or *Galago* but, in spite of their greater size, retain many of the primitive features of brain and skull. Elliot Smith says: "The cerebral features of the members of the genera *Lemur* and *Hapalemur* (i.e., *Myoxicebus*) are not far removed from those of *Galago*." Nineteen is their characteristic number of thoracolumbar vertebrae. *Lepidolemur* also with nineteen thoracolumbar vertebrae is in some ways more specialized towards the pithecoïd type, in other ways more primitive than *Lemur* itself. The single instance in which the thoracolumbar vertebrae of *Lemur* number twenty finds its explanation in the lemuroid tendency to lengthening of the column. The solitary case in which the number is only eighteen can be understood upon reference to the section of this chapter dealing with the non-lemurine Primates.

We now pass to the next group, namely, the Chirogaleinae. Of these *Myoxicebus* itself differs very little in its brain from *Lemur*, although it may be that *Myoxicebus* shows a slightly nearer approach to the pithecoïd type. The records of skull and dentition accord almost in detail with this, for my notes state that it shows "altogether about the same amount of specialization as *Lemur* though along a rather different line." As a result, we are quite prepared to find that the thoracolumbar number is eighteen, and not nineteen or twenty. *Microcebus*, unfortunately, receives no clear statement. Elliot Smith points out



similarities to Lemur and to the Lorissinae, but does not commit himself. My notes state in part: "Palate approaching Lemur type. Upper central incisor still large as in Insectivora. Premolars and molars fairly generalized. I am very uncertain about this beast." It may be that *Microcebus* is more specialized than *Myoxicebus* and perhaps somewhat retrogressive. This would accord quite well with the twenty thoracolumbar vertebrae.

Finally we deal with the very specialized families Indrisinae and Daubentonidae. Towards the former, according to Elliot Smith, *Lepidolemur* points the way. Of these undoubtedly *Propithecus* is least specialized, then *Indris* and, most specialized of all, *Lichanotus*. Again this agrees with the increasing number of vertebrae, namely, twenty in *Propithecus* and twenty-one in the others.

*Daubentonia*, in spite of its retrogressive features, shows clear evidence of its origin from a very Lemur-like type specialized along the lines of the Indrisinae. My notes state that there are some evidences of a pithecoïd tendency. This gives added weight to the rather striking fact that the number of thoracolumbar vertebrae has not increased as in the Indrisinae, but remains nineteen.

I have dealt somewhat at length with the problem of numerical variation of vertebrae in the lemurs because I desire to make clear the argument for a significant and not accidental phylogenetic trend in the vertebral column and thus pave the way for a more definite understanding of the types of variation in the lower lumbar column of man. Matthew, in discussing the species of *Notharctidae* from the successive geological horizons of the lower and middle Eocene, makes the following very illuminating statement (15:

As with other abundant groups, a large series shows a certain range of individual variation, some being more and others less progressive, but within comparatively narrow limits. As we progress upward through successive levels of the formations, we find that the limits of individual variation, on one side or the other of the abundant typical forms, are progressively shifted over in the direction of the phyletic trend. That this is a gradual shifting of averages, due to the disap-

pearance of less progressive individuals, and appearance and increase of more progressive individuals, seems to be fairly well shown in this dhyllum [i.e. *Notharctus* and *Pelycodus*. T.W.T.] . . . It is not the gradual replacement of one species by another distinct and more progressive species, but so far as one may judge from the characters of the teeth the gradual conversion of one species into its successor by the progressive elimination of the more primitive and increase in numbers of the more advanced individuals.

What we are now in effect looking at are the terminal stages of the progression, one animal after another representing a phase or offshoot along the general phylogenetic trend. In the lemurs we note in the main a trend towards lengthening of the thoracicolumbar column as in most other mammalian orders. But here and there we find a suggestion of another type of trend, namely, towards actual shortening of the column. It is this type, barely suggested in the lemurs, which we shall find ever more and more strongly evidenced as we pass in review the successively higher groups of non-lemurian Primates.

#### THE THORACICOLUMBAR VERTEBRAE IN THE NEW-WORLD MONKEYS

If we arrange the columns of the New-World monkeys in order, commencing with those in which nineteen thoracicolumbar vertebrae are characteristic, we find the following notable results:

##### Hapalidae:

|                                      |        |         |      |
|--------------------------------------|--------|---------|------|
| <i>Oedipomidas oedipus</i> Linnaeus. | T+L 19 | R.C.S., | 244. |
| <i>Callithrix jacchus</i> Linnaeus.  | T+L 19 | R.C.S., | 246. |
| <i>Callithrix jacchus</i> Linnaeus.  | 19     | R.C.S., | 247. |
| <i>Callithrix jacchus</i> Linnaeus.  | 19     | R.C.S., | 249. |

##### Cebidae:

###### *Cebus*:

|                               |        |            |      |
|-------------------------------|--------|------------|------|
| <i>C. capucinus</i> Linnaeus. | T+L 19 | R.C.S.,    | 208. |
| <i>C. capucinus</i> Linnaeus. | 20     | R.C.S.,    | 209. |
| <i>C. capucinus</i> Linnaeus. | 19     | R.C.S.,    | 214. |
| <i>C. capucinus</i> Linnaeus. | 19     | R.C.S.,    | 215. |
| <i>C. unicolor</i> Spix.      | T+L 19 | W.R.U., B. | 142. |

##### *Pithecia*:

|                                |        |         |      |
|--------------------------------|--------|---------|------|
| <i>P. monacha</i> E. Geoffroy. | T+L 19 | R.C.S., | 230. |
|--------------------------------|--------|---------|------|

##### *Alouatta*:

|                               |        |            |      |
|-------------------------------|--------|------------|------|
| <i>A. palliata</i> Gray.      | T+L 20 | W.R.U., B. | 340. |
| <i>A. seniculus</i> Linnaeus. | T+L 18 | R.C.S.,    | 235. |

##### *Ateles*:

|                                  |        |            |      |
|----------------------------------|--------|------------|------|
| <i>A. geoffroyi</i> Kuhl.        | T+L 18 | R.C.S.,    | 217. |
| <i>A. belzebuth</i> E. Geoffroy. | T+L 17 | W.R.U., B. | 141. |

*Lagothrix*:

|                         |        |         |      |
|-------------------------|--------|---------|------|
| L. lagotricha Humboldt. | T+L 18 | R.C.S., | 226. |
|-------------------------|--------|---------|------|

*Saimiri* (*Chrysothrix*):

|                       |        |         |      |
|-----------------------|--------|---------|------|
| S. sciureus Linnaeus. | T+L 20 | R.C.S., | 202. |
|-----------------------|--------|---------|------|

|                       |    |         |      |
|-----------------------|----|---------|------|
| S. sciureus Linnaeus. | 20 | R.C.S., | 203. |
|-----------------------|----|---------|------|

|                       |    |         |      |
|-----------------------|----|---------|------|
| S. sciureus Linnaeus. | 20 | R.C.S., | 204. |
|-----------------------|----|---------|------|

|                         |    |         |         |
|-------------------------|----|---------|---------|
| S. oerstedii Reinhardt. | 20 | W.R.U., | B. 341. |
|-------------------------|----|---------|---------|

*Aotus* (*Nyctipithecus*):

|                     |        |         |      |
|---------------------|--------|---------|------|
| A. vociferans Spix. | T+L 22 | R.C.S., | 227. |
|---------------------|--------|---------|------|

|                     |        |         |         |
|---------------------|--------|---------|---------|
| A. gularis Dollman. | T+L 21 | W.R.U., | B. 342. |
|---------------------|--------|---------|---------|

We cannot attempt to follow out in detail the relationships of these animals the one to the other. Suffice is to say that all tend toward specialization of a rather pronounced nature, but that *Cebus* itself occupies a central position among Primates generally (Elliot Smith, 3, p. 399). From the typically primitive mammalian number as shown characteristically by *Cebus*, we note two trends of variation. The one evidenced by *Saimiri* and *Aotus* is towards lengthening, as occurs almost exclusively among the lemurs. The other exhibits a more or less marked tendency towards shortening. This trend was seen only in *Lemur* and *Myoxicebus* among the lemurs. For our present purpose the New-World monkeys are significant in that while their brain shows a very close affinity with that of the lemurs, their vertebral column presents a stage distinctly intermediate between those of the lemurs and of the higher apes.

THE THORACICOLUMBAR VERTEBRAE OF THE OLD-  
WORLD APES

In contradistinction to the two types of trend shown by the *Cebidae*, the thoracicolumbar column of the *Cercopithecidae* presents a remarkable stability in both the subfamilies.

*Subfamily Lasiopyginae*

|                                 |        |         |         |
|---------------------------------|--------|---------|---------|
| <i>Lasiopyga mona</i> Schreber. | T+L 19 | W.R.U., | B. 147. |
|---------------------------------|--------|---------|---------|

|                                          |        |         |      |
|------------------------------------------|--------|---------|------|
| <i>Lasiopyga griseoviridis</i> Demarest. | T+L 19 | R.C.S., | 112. |
|------------------------------------------|--------|---------|------|

|                                     |        |         |      |
|-------------------------------------|--------|---------|------|
| <i>Lasiopyga albigularis</i> Sykes. | T+L 19 | R.C.S., | 118. |
|-------------------------------------|--------|---------|------|

|                                       |        |         |      |
|---------------------------------------|--------|---------|------|
| <i>Lasiopyga petaurista</i> Schreber. | T+L 19 | R.C.S., | 124. |
|---------------------------------------|--------|---------|------|

|                      |        |         |      |
|----------------------|--------|---------|------|
| <i>Lasiopyga</i> sp. | T+L 19 | R.C.S., | 108. |
|----------------------|--------|---------|------|

|                                     |        |         |      |
|-------------------------------------|--------|---------|------|
| <i>Erythrocebus patas</i> Schreber. | T+L 19 | R.C.S., | 109. |
|-------------------------------------|--------|---------|------|

|                                  |        |         |         |
|----------------------------------|--------|---------|---------|
| <i>Pithecus rhesus</i> Audebert. | T+L 19 | W.R.U., | B. 460. |
|----------------------------------|--------|---------|---------|

|                                  |        |         |         |
|----------------------------------|--------|---------|---------|
| <i>Pithecus rhesus</i> Audebert. | T+L 19 | W.R.U., | B. 148. |
|----------------------------------|--------|---------|---------|

|                                  |        |         |      |
|----------------------------------|--------|---------|------|
| <i>Pithecus rhesus</i> Audebert. | T+L 19 | R.C.S., | 151. |
|----------------------------------|--------|---------|------|



|                                       |        |            |      |
|---------------------------------------|--------|------------|------|
| <i>Pithecus rhesus</i> Audebert.      | T+L 19 | R.C.S.,    | 152. |
| <i>Pithecus rhesus</i> Audebert.      | T+L 19 | R.C.S.,    | 153. |
| <i>Pithecus rhesus</i> Audebert.      | T+L 19 | R.C.S.,    | 154. |
| <i>Pithecus rhesus</i> Audebert.      | T+L 19 | R.C.S.,    | 155. |
| <i>Pithecus nemestrinus</i> Linnaeus. | T+L 19 | W.R.U., B. | 337. |
| <i>Pithecus nemestrinus</i> Linnaeus. | T+L 19 | R.C.S.,    | 160. |
| <i>Pithecus fascicularis</i> Raffles. | T+L 19 | R.C.S.,    | 135. |
| <i>Pithecus fascicularis</i> Raffles. | T+L 19 | R.C.S.,    | 136. |
| <i>Pithecus fascicularis</i> Raffles. | T+L 18 | R.C.S.,    | 134. |
| <i>Pithecus pileatus</i> . Kerr.      | T+L 19 | R.C.S.,    | 144. |
| <i>Pithecus sinicus</i> Linnaeus.     | T+L 19 | R.C.S.,    | 145. |
| <i>Simia sylvanus</i> Linnaeus.       | T+L 19 | R.C.S.,    | 170. |
| <i>Theropithecus gelada</i> Rüppell.  | T+L 19 | R.C.S.,    | 178. |
| <i>Theropithecus gelada</i> Rüppell.  | T+L 19 | R.C.S.,    | 179. |
| <i>Papio cynocephalus</i> Linnaeus.   | T+L 19 | R.C.S.,    | 184. |
| <i>Papio</i> sp.                      | T+L 19 | R.C.S.,    | 187. |
| <i>Papio porcarius</i> Brunnich.      | T+L 19 | R.C.S.,    | 192. |
| <i>Papio leucophaeus</i> F. Cuvier.   | T+L 19 | R.C.S.,    | 196. |
| <i>Papio sphinx</i> . Linnaeus.       | T+L 18 | R.C.S.,    | 198. |
| <i>Papio</i> sp.                      | T+L 19 | W.R.U., B. | 151. |

*Subfamily Colobinae:*

|                                        |        |            |      |
|----------------------------------------|--------|------------|------|
| <i>Pygathrix entellus</i> Dufrèsne.    | T+L 19 | W.R.U., B. | 158. |
| <i>Pygathrix entellus</i> Dufrèsne.    | T+L 19 | R.C.S.,    | 83.  |
| <i>Pygathrix entellus</i> Dufrèsne.    | T+L 19 | R.C.S.,    | 90.  |
| <i>Pygathrix rubicunda</i> Müller.     | T+L 19 | W.R.U., B. | 622. |
| <i>Pygathrix schistaceus</i> Hodgson.  | T+L 19 | R.C.S.,    | 96.  |
| <i>Pygathrix cristata</i> Raffles.     | T+L 19 | R.C.S.,    | 100. |
| <i>Nasalis larvatus</i> Wurm.          | T+L 18 | R.C.S.,    | 105. |
| <i>Nasalis larvatus</i> Wurm.          | T+L 19 | R.C.S.,    | 107. |
| <i>Colobus vellerosus</i> I. Geoffroy. | T+L 19 | R.C.S.,    | 78.  |

Now the striking fact to be observed in these animals beyond the constancy of the number nineteen is the fact that when variation does occur it is, in both subfamilies, a reduction to eighteen. We note, then, that no longer is the general mammalian trend towards elongation to be found. In this respect the lemurs are distinctly the link with mammals generally. The Cebidae occupy an intermediate position between the far more typically mammalian lemurs and the distinctively primate Old-World apes. We shall see the same sort of intermediate part taken by the small anthropoid *Hylobates* between the giant anthropoids and the Old-World apes.

## THE THORACICOLUMBAR VERTEBRAE IN THE ANTHROPOIDS

In considering the anthropoids one must separate the gibbons from the giant apes. The former are exceedingly like the Cercopithecidae in many respects and, a priori, would be expected to show a vertebral formula close to that of the Old-World apes. The giant anthropoids, on the contrary, are very specialized, more specialized in many ways than in Man himself. The ensuing tables show plainly that the vertebral formula of the several anthropoids confirms these general impressions.

## Hylobatidae:

|                                     |        |         |         |
|-------------------------------------|--------|---------|---------|
| Hylobates concolor Harlan.          | T+L 18 | W.R.U., | B. 160. |
| Hylobates concolor Harlan.          | 18     | W.R.U., | B. 162. |
| Hylobates concolor Harlan.          | 17     | W.R.U., | B. 161. |
| Hylobates lar Linnaeus.             | 18     | R.C.S., | 65.     |
| Hylobates lar Linnaeus.             | 18     | R.C.S., | 66.     |
| Hylobates sp.                       | 18     | R.C.S., | 63.     |
| Hylobates hoolock Harlan.           | 17     | W.R.U., | B. 159. |
| Symphalangus syndactylus Desmarest. | T+L 17 | R.C.S., | 58.     |
| Symphalangus syndactylus Desmarest. | 17     | R.C.S., | 61.     |

## Giant Anthropoids:

|     |        |         |         |
|-----|--------|---------|---------|
| Pan | T+L 17 | W.R.U., | B. 168. |
|     | 17     | W.R.U., | B. 346. |
|     | 17     | W.R.U., | B. 347. |
|     | 17     | W.R.U., | B. 543. |
|     | 17     | W.R.U., | B. 632. |
|     | 16     | W.R.U., | B. 171. |
|     | 16     | W.R.U., | B. 540. |
|     | 17     | R.C.S., | 1       |
|     | 17     | R.C.S., | 13      |
|     | 16     | R.C.S., | 4       |
|     | 16     | R.C.S., | 5       |

## Gorilla

|  |        |         |         |
|--|--------|---------|---------|
|  | T+L 17 | W.R.U., | B. 168. |
|  | 17     | W.R.U., | B. 239. |
|  | 17     | W.R.U., | B. 624. |
|  | 16     | W.R.U., | B. 169. |
|  | 16     | W.R.U., | B. 626. |
|  | 16     | W.R.U., | B. 627. |
|  | 17     | R.C.S., | 20      |
|  | 17     | R.C.S., | 23      |
|  | 17     | R.C.S., | 29      |
|  | 17     | R.C.S., | 30      |
|  | 16     | R.C.S., | 21      |

|       |     |    |         |    |      |
|-------|-----|----|---------|----|------|
| Pongo | T+L | 16 | W.R.U., | B. | 164. |
|       |     | 16 | W.R.U., | B. | 172. |
|       |     | 16 | W.R.U., | B. | 623. |
|       |     | 16 | W.R.U., | B. | 624. |
|       |     | 17 | R.C.S., |    | 37   |
|       |     | 16 | R.C.S., |    | 38   |
|       |     | 16 | R.C.S., |    | 40   |
|       |     | 16 | R.C.S., |    | 50   |
|       |     | 16 | R.C.S., |    | 51   |

The same process of reduction which is characteristic of the Old-World apes becomes still more striking among the anthropoids. Of the gibbons the less specialized show eighteen or seventeen thoracicolumbar vertebrae and of the two skeletons of the more highly specialized *Symphalangus* each possesses only seventeen. In the giant anthropoids the number seventeen is more characteristic of the great black anthropoids, as it is of Man. In these animals, much more than in Man, there is a tendency to reduction to sixteen. This reduction to sixteen becomes characteristic of the very specialized Orang, Pongo. In this general manner we may read the tables at a glance; it will, however, be profitable to consider them a little more closely.

Keith's table III (13, p. 24) is very illuminating and in point of number greatly exceeds ours. The specimens from the College of Surgeons are included both in my tables and in Keith's. If, then, we reduce to actual numbers the percentages in Keith's table and add those skeletons belonging to the Hamann Museum, a composite statement can be set forward. For the statistics upon Man in Keith's table I have substituted the figures obtained by Willis (20) in this laboratory as being probably less selected. Of course it must be understood that Willis' figures refer to a mixture of White and Negro races and both sexes. For further details the reader should consult the original paper.

There is no doubt about the progressive reduction in number with such a table to hand and there is likewise no doubt concerning the relative position of Man in the progression. Reduction has gone distinctly further in the giant anthropoids and has left Man sensibly nearer the gibbons.



*Number of thoracicolubar vertebrae*

|             | TOTAL | 15 | 16 | 17  | 18 | 19 |
|-------------|-------|----|----|-----|----|----|
| Orangs      | 50    | 3  | 39 | 8   |    |    |
| Gorillas    | 33    | 2  | 13 | 18  |    |    |
| Chimpanzees | 45    | 1  | 10 | 26  | 8  |    |
| Man         | 748   |    | 5  | 717 | 26 |    |
| Gibbons     | 63    |    |    | 11  | 48 | 4  |

That the primitive number nineteen is not exceeded in either subfamily of Old-World apes appears both from the Reserve material and from the skeletons in the College of Surgeons. But Keith has indicated that an increase to twenty does occasionally appear in *Pithecus* and more frequently in *Papio*. One would not deny the existence of this increase, relatively infrequent though it is. However, it must be borne in mind that prepared skeletons supplied by dealers or macerated by inexperienced preparators not rarely show evidence of tampering with the vertebral column, which is either composite or lacks one or more vertebrae. I am therefore not prepared to pay much attention to outlying stragglers. Another difficulty met when one attempts arbitrarily to assign vertebral columns to definite figures, which necessarily imply a greater degree of definition than actually occurs in the column itself, is that of the lumbosacral vertebra in its several degrees. There may quite justly be a difference of opinion as to its exact position in the column.

In his investigation of our material Willis found it worth while to separate on the one hand those columns showing distinctly and unquestionably sixteen, seventeen, or eighteen thoracicolubar vertebrae, and on the other the intermediate types. Consequently, he found that the statements as given in the table above by no means represent the real condition of the human column. In addition to the five specimens possessing only sixteen thoracicolubars there were thirty-five showing an abmodal condition approximating sixteen. Also beyond the twenty-six with eighteen thoracicolubars there were fifteen abmodal examples which might well be considered as tending distinctly towards eighteen. If, then, these imperfect types be added to the perfect examples, the distribution is changed to the following:

Sixteen T-L, 40. Seventeen T-L, 667. Eighteen T-L, 41.

Going into this matter still further, Willis finds that, considering each tendency to reach complete definition at 100 per cent, the tendency towards the presumably ancestral eighteen is expressed by 63.4 per cent of the abmodals reaching complete definition and only 36.6 per cent remaining partial or incomplete. The tendency towards sixteen is expressed by only 12.5 per cent reaching complete definition; 87.5 per cent. the great majority, remaining incomplete. Now this is a much happier method of presenting the progression as shown in Man. No doubt if such a scheme could be adopted for the other Primates we should have just as enlightening a description of what has taken place in them. Meantime we must content ourselves with such an imperfect arrangement as I have given in my table above. All that can actually be deduced is that seventeen is the modal number for Man and the giant black anthropoids, whereas eighteen is modal for the small and Old-World ape-like gibbons, and sixteen for the Orang. It may, however, be inferred with some reason that in the Chimpanzee, as in Man, there is about equal tendency towards eighteen and sixteen thoracicolumbars, although from the frequency of expression of this tendency in the Chimpanzee it is apparent that the column of that ape is in a much more unstable condition than the column of Man. The Gorilla has progressed further along the line of specialization and appears to exhibit no tendency towards eighteen. The Orang is fairly definitely settled with sixteen.

The really noteworthy fact is that the column of Man is remarkably stable numerically as compared with the columns of his near relatives, so far as we are able to obtain detailed information. This appears very clearly indeed in Willis' careful discussion.

The relative stability in White and Negro races is a problem to be taken up later. Judging from other studies upon the human skeleton, we must be prepared to find no evidence of a 'lower' or a 'higher' race, but rather a humanoid specialization more marked in the Negro than in the White.

Now, in summary of the foregoing observations, we may note several points. It is not necessary to obtain the entire number of vertebral segments including the tail or coccyx to enable one to come to a decision concerning transmutation of vertebral segments during phylogeny. We have seen that the Primates differ from most other mammalian orders in that there is expressed a tendency towards reduction in number of the thoracolumbar vertebrae, and that this appears as Rosenberg, Welcker, and others have perceived. The lemurs plainly form the connecting link between Primates and other mammals in this respect as in so many others, and the New-World monkeys stand distinctly closer to the lemurs than to the Old-World apes. The vertebral column of the Old-World apes shows clearly its basic relation to the stem wherefrom successively the gibbons, Man, the giant black anthropoids and the Orang diverged, with concomitant reduction in number of the thoracolumbar vertebrae. The facts presented here merely serve to confirm these assertions already made. We have carried out the investigation somewhat more searchingly, however, and as a result have found that the number of thoracolumbars bears an interesting relation to the degree of specialization of the genus. We have been able to follow out this line of thought more particularly among the lemurs and the anthropoids, which groups are in reality most essential for the fundamental accuracy of the general concept. Various suggestive features of the studies by Keith and by Bardeen indicate the correlation between transmutation of the vertebrae and the spinal nerves and plexuses. Hence our next step is the presentation of results of investigation in this laboratory concerning degree of transmutation of vertebrae compared with the constitution of the nerves and plexuses in the same individuals.

#### SUMMARY

1. The following accepted ideas regarding the presacral vertebral column in mammals are undoubtedly correct. The primitive mammalian number of thoracolumbar vertebrae is and always has been nineteen. In most orders of mammals there is a tendency to increase this number (Welcker's auxispondylous



group). In Primates the tendency is to reduce the number, the anthropoids and Man forming Welcker's lipospondylous group. So far as the thoracicolumbar column is concerned, Man takes his place between the gibbons and the giant black anthropoids.

2. The lemurs form the connecting link between the Primates and other mammalian orders. Whereas some in their specialization exhibit an increase in number like the auxispondylous mammals, there are others which lean towards the typically higher Primates in their tendency towards reduction in number of thoracicolumbar vertebrae. The relation of vertebral formula to specialization in the lemurs is quite significant.

3. The New-World monkeys show a greater tendency towards reduction in number, but here also there is marked bias towards increase in number, as in many lemurs.

4. The primitive number nineteen is characteristic of both subfamilies of Old-World apes, only rare examples showing an increase to twenty.

5. The anthropoids and Man exhibit progressive reduction in number, but of all this group man presents by far the most stable condition numerically in his vertebral formula. The precise stability for Man is strikingly given in the recent work by Willis.

#### LITERATURE CITED

- 1 COOTE, H. 1849 Homologies of the human skeleton. London.
- 2 ELLIOT, D. G. 1913 A review of the Primates. Monograph no. 1. Am. Mus. Nat. Hist., 3 vols. New York.
- 3 ELLIOT SMITH, G. 1902 Cat. Physiol. Series., Mus. Roy. Coll. Surg., vol. 2, 2nd ed.
- 4 1903 On the morphology of the brain in the Mammalia with special reference to that of the Lemurs, recent and extinct. Trans. Linn. Soc., second series, Zoology, vol. 8, pp. 319-432.
- 5 FLOWER, W. H. 1884 Osteological Catalogue of the Royal College of Surgeons. Part II, Mammalia.
- 6 1885 Osteology of the Mammalia. London, 3rd ed.
- 7 GREGORY, W. K. 1910 The Orders of Mammals. Bull. Amer. Mus. Nat. Hist., vol. 27, pp. 1-524.
- 8 1910 Notes on the insectivore genus *Tupaia* and its allies. Science, vol. 31, pp. 918-919.
- 9 1913 Relationship of the Tupaiidae and of Eocene lemurs, especially *Notharctus*. Bull. Geol. Soc. America, vol. 24, pp. 241-252.
- 10 1915 On the relationship of the Eocene lemur *Notharctus* to the Adapidae and to other Primates. Bull. Geol. Soc. America, vol. 26, pp. 419-446.

- 11            1920    On the structure and relations of *Notharctus*, an American Eocene Primate. *Mem. Amer. Mus. Nat. Hist.*, new series, vol. 3, pp. 49-243.
- 12 HUXLEY, T. H. 1880    On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proc. Zool. Soc.*, 1880, pp. 649-662.
- 13 KEITH, A. 1902    The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of Man and allied Primates. *Journ. Anat. and Physiol.*, vol. 37, pp. 18-40.
- 14 MATTHEW, W. D. 1904    The arboreal ancestry of the Mammalia. *Amer. Naturalist*, vol. 38, pp. 811-818.
- 15 MATTHEW, W. D., AND GRANGER, W. 1915    A revision of the lower Eocene Wasatch and Wind River faunas. *Bull. Amer. Mus. Nat. Hist.*, vol. 34, pp. 429-483.
- 16 OWEN, R. 1866.    The anatomy of Vertebrates. London, vol. 2.
- 17 PATERSON, A. M. 1892    The human sacrum. *Proc. Roy. Soc.*, vol. 51, pp. 520-524.
- 18 ROSENBERG, E. 1876    Ueber die Entwicklung der Wirbelsäule und das Centrale carpi des Menschen. *Morph. Jahrb.*, Bd. 1, S. 83-197.
- 19 WELCKER, H. 1881    Die neue anatomische Anstalt zu Halle durch einen Vortrag über Wirbelsäule und Becken. *Arch. f. Anat. u. Entwicklungsgesch.*, Jahrg. 1881, S. 161-192.
- 20 WILLIS, T. A. 1923    The lumbo-sacral vertebral column. *Am. Jour. Anat.*, vol. —, pp. —.





Resumen por el autor, G. S. Dodds.

El área de las vellosidades coriónicas en  
la placenta a término.

Un niño recién nacido fué objeto de medidas, calculándose después el área de superficie expuesta por las vellosidades coriónicas a la acción de la sangre materna. El método empleado se basa en el estudio de preparaciones microscópicas, calculándose primero el área de las porciones de las vellosidades incluídas en una sección determinada, y con estos datos se calculó su área total para la placenta. El área así determinada mide unos siete metros cuadrados.

Translation by José F. Nonidez  
Cornell Medical College. New York.

## THE AREA OF THE CHORIONIC VILLI IN THE FULL TERM PLACENTA

G. S. DODDS

*West Virginia University*

THREE FIGURES

When studying the placenta with classes in embryology, the question has often arisen as to the extent of the surface presented by the chorionic villi to the maternal blood in the intervillous blood space—that is, the surface through which exchange of materials between maternal and fetal blood takes place. If such computations have previously been made, I am not aware of them. No figures of such areas are given in the text-books with which I am familiar, and it is with the hope that the facts may be as new to many other embryologists as to myself that without extensive search of the literature I venture to publish the result of my computations.

As is well known, the placenta consists of the chorion frondosum (fetal part of the placenta) and the decidua basalis (maternal part), a portion of the uterine mucosa. The chorion bears numerous villi which branch extensively in the intervillous blood space which lies between the chorion and the uterine wall. The trunks of some of the attaching or anchoring villi are surrounded by or adherent to the decidua, but by far the greater number, including thousands of small branches, float freely in the blood space, bathed continually with the maternal blood. Through the surface of these villi exchanges of materials take place between the maternal blood in the sinus and the fetal blood which circulates through the villi in the branches of the umbilical arteries and veins.

The following calculations are based upon the study of a single human afterbirth of about average size, one of those in the collection used for demonstration to my classes. On account of

various sources of error to be mentioned later, the figures given are but an approximation, though a very useful one, and I believe no advantage would be gained by the study of more specimens.

The placenta in question (fig. 1) had an outline approximately circular, with a diameter of 16 cm. and an average thickness of about 2.5 cm. The placenta had undoubtedly undergone some shrinkage during the formalin perservation and so is somewhat less in volume than when fresh, but this difference will not so much affect the final result as to greatly lessen its value. The volume, as near as could be computed, was 502 cc., though irregularities of form made such methods rather inaccurate. A more accurate figure, 510 c.c. was obtained by displacement of

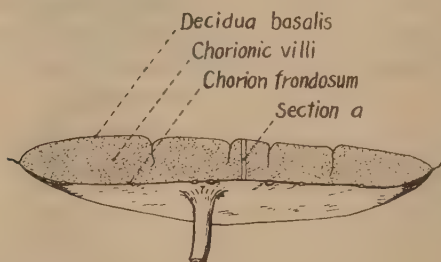


Fig. 1 Placenta cut vertically near its greatest diameter. Position of section from which measurements were made is shown by unshaded band.

water, and has been used the calculations to follow. Of this volume a small part is taken up by the chorion frondosum on one surface and the decidua basalis on the other, with a combined thickness of about 1 mm. (4 per cent of the thickness of the placenta). Making this deduction, about 490 cc. remains as the volume of the blood sinus in which the villi are contained.

#### METHOD

The measurements and calculations are made from microscopic sections as follows: First the parts of villi in a section  $10\ \mu$  thick, extending across the placenta from chorion to decidual surface, were measured and the total surface area of the portion of villi included in this section computed (fig. 1, *a*). From this was



determined the surface area of the villi in 1 cu. mm. of similar tissue, and from this their surface area in the whole placenta.

The details of procedure are as follows: The whole section including 2,294 sections or slices of villi, was drawn to a known scale by the use of a microprojection lantern. The slices of villi are of various sizes and shapes, as in figure 2, which is a drawing

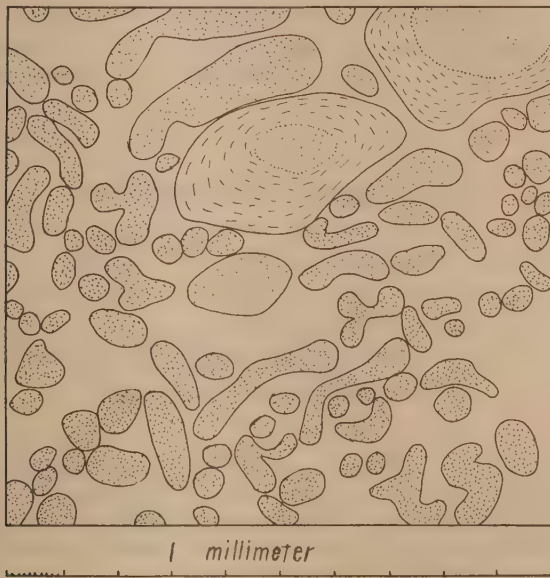


Fig. 2 Part of drawing on which villi were measured, 1 sq.mm. of section included. The rounded stippled areas represent villi cut directly across, the elongated ones those cut diagonally at various angles. The two villi marked partly with line shading are those covered with 'canalized fibrin' and not included in the computed area.

of 1 sq. mm. of the section. The shaded areas represent slices of villi which are of somewhat different sizes, run in all directions, are crooked, and branch richly. The slices of villi in the section would appear, if seen in perspective as shown in Figure 3, *a*, *b*, *c*, which represent sections of cylinders of the same diameter cut at different angles, and when seen from directly above, as under the microscope like *a'*, *b'*, *c'*. The size and shape of the slice

depend not only on the size of the villus, but also on the direction in which it is cut. To compute the surface area of a single slice of a villus is easy, provided it is cut directly across as in figure 3, *a*, where the circumference or perimeter of the slice multiplied by the thickness of the section gives the surface area (the area of the surface shaded with lines in fig. 3, *a*). But when the villus is cut obliquely as in 3, *b* and *c*, the product of the perimeter by the thickness of the section is somewhat less than the actual area, because of the slanting surface at the end of the elliptical sections. In practice, however,

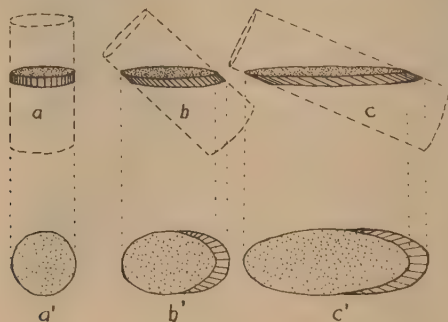


Fig. 3 Diagram to show cylinders of same diameter cut at various angles. *a*, *b*, *c*, showing sections in perspective, *a'*, *b'*, *c'*, projections of these sections, such as the sections of villi as seen in the microscopic section. The part shaded with lines represents the area to be measured, and roughly equals the product of the perimeter of the section by its thickness.

this would probably not be a serious error, because in thin sections, such as actually used, the slanting end shown by the lined surface in figure 3, *b'* and *c'*, is small, and in making the drawing would usually be covered by the width of the line, and so would be within the limit of error of the method employed. We may conclude that the error is not great if we assume that to measure any slice of villus in the section we have but to take the product of the perimeter of the slice by its thickness. This method gives a pretty good approximation of the correct figure, and any constant error is of a negative sign, i.e., the computed area is somewhat less than the actual.

In practice it is not necessary to make separate calculation of the surface area of each villus in the section, but merely to ascertain their combined perimeter and multiply this sum by the thickness of the section and thus obtain the total surface area of all the slices in the section.

The measurements of the drawn slices of villi were made by using a map measurer, an instrument having a small wheel with which to trace the line to be measured, geared to a hand which registers on a dial the distance. Considerable shrinkage takes place during the paraffin imbedding, as shown by measurement before and after. Allowance is made for this in all the linear measurements, and the figures given below are those after this correction has been made.

In making the measurements, care was taken to include only those villi which seemed to have a surface suitable for absorption, that is, those covered with thin, syncytial epithelium, and to exclude those covered with 'canalized fibrin,' these latter mostly of large size, evidently the main trunks from which the smaller ones arise. These smaller ones we will call 'absorbing' villi.

*Measurements of placenta*

|                                                                 |         |         |
|-----------------------------------------------------------------|---------|---------|
| Diameter . . . . .                                              | 160     | mm.     |
| Average thickness . . . . .                                     | 25      | mm.     |
| Volume by calculation . . . . .                                 | 502,000 | cu.mm.  |
| Volume by water displacement . . . . .                          | 510,000 | cu.mm.  |
| Volume of blood sinus (510,000 less 4 per cent) . . . . .       | 490,000 | cu.mm.  |
| Area of section drawn and measured . . . . .                    | 60.14   | sq. mm. |
| Thickness of section drawn and measured, 10 $\mu$ , or 0.01 mm. |         |         |

*Measurements of drawing of section*

|                                                         |             |
|---------------------------------------------------------|-------------|
| Number of absorbing villi in section . . . . .          | 2,294       |
| Total perimeter of absorbing villi in drawing . . . . . | 124,400 mm. |
| Magnification of drawing . . . . .                      | 155 diam.   |
| Actual perimeter of villi <u>124,400</u> . . . . .      | 802.5 mm.   |
|                                                         | 155         |

From these figures one may compute the total surface area of villi in the whole placenta as follows:

Area of absorbing villi in measured section:

$$802.5 \times .01 \text{ mm.} = 8.025 \text{ sq.mm.}$$

Volume of measured section:

$$60.14 \text{ sq.mm.} \times .01 \text{ mm.} = .6014 \text{ cu.mm.}$$

Area of absorbing villi per cubic millimeter of material like that composing the section:

$$\frac{8.025}{.6014} = 13.3438 \text{ sq.mm.}$$

Total area of all absorbing villi in placenta:

$$13.3438 \times 490,000 = 6,538,462 \text{ sq.mm.}$$

6.5 sq.meters  
69.94 sq.ft.

This area, as previously pointed out, does not include the total surface exposed within the placenta, but only that of the small villi which, on account of their size and the nature of their surface, seem suited to function as absorbing structures. There is omitted from the above area the surface of those villi, mostly large ones, covered with fibrous or hyaline material, the surface of the decidual septa, and the inner surfaces of decidua basalis and chorion frondosum. From measurements made in the same way as for the smaller villi, it appears that these surfaces include nearly  $\frac{1}{10}$  of the total internal surface of this placenta, which thus is about 7 square meters.

The functional surface of the absorbing villi is doubtless reduced somewhat by the numerous thickenings in their epithelium in the form of masses of nuclei, variously known as 'proliferation islands,' 'nuclear groups,' etc., and by the crowding of villi, so that surfaces of adjacent villi are in contact and thus not freely exposed to the maternal blood. Thus it appears that the effective, absorbing surface within the placenta includes not the total of 7 square meters, nor the measured area of the absorbing villi, 6.5 square meters, but a figure somewhat less than this and hard to estimate.

Inasmuch as the above calculations are based upon measurements of but one section with an area of 60.14 sq.mm., sections



from other parts of the placenta were studied, the number of villi per sq.mm. counted and measures of the size of these villi taken. From these observations it seems that the section which forms the basis of these figures is representative, and no great difference would appear if several sections were measured. That is, in any section of this size, no matter from what part of the placenta it is cut, we find about the same number of villi per sq.mm. and the average size of the villi cut is remarkably constant.

Concerning the method used, it is to be noted that though the actual microscopic section was cut  $10\ \mu$  thick, the result would have been the same had it been 5 or  $15\ \mu$  or any other thickness, because the slices of villi in the section are assumed to be cross-sections of various shaped bodies extending in a direction perpendicular to the plane of the section not only within the section, but indefinitely outside the section to the border of the placenta. Not only this, but all the villi of the placenta are assumed to be straight, parallel bodies of the same average size as those measured. The element of truth in this assumption is that in any section cut, there appear as many villi, and of the same size, as in the one measured, though not the same villi. The element of error is the oblique direction taken by many of the villi in the section, which makes their actual area less than the computed area.

The result of 6.5 square meters (70 sq.ft.) is so large as at first to seem unreasonable. In order to try to surprise myself into inconsistencies, I tried several modifications of the method and always arrived at the same result. Certain figures from such calculations may be of interest: the average number of villi cut per sq. mm. was 38, in some areas running to a number above 100, in others much fewer on account of less dense arrangement and presence of large trunks of villi. In a complete vertical section across the placenta there would be cut 133,760 villi, and in a complete horizontal section 763,648. The average perimeter of the sections of absorbing villi measured is 0.357 mm.—a figure from which there is a surprisingly small deviation when any area as large as 1 sq.mm. is measured. A villus of

this average size and with a surface area of 6.5 square meters would have a length of a little more than 18 kilometers ( $11\frac{1}{4}$  miles). Lest this measure may seem excessive, we note that a cylinder of this length and area will have a diameter of 0.113 mm., and occupies a volume of 174,000 cu.mm. (174 cc.), about 37 per cent of the volume of the blood sinus in which the villi actually float, leaving 63 per cent of the space for the circulation of the maternal blood—a relation which, from a general inspection of the sections, seems not unreasonable.

As a matter of fact, the diameter of this 'average' villus (0.113 mm.) is larger than the actual free terminal branches of the absorbing villi, because many of these sections are oblique, and also a few of the larger trunks are included in the measured sections. The diameters of these free villi, as actually measured both on an enlarged drawing and on the sections, fall mostly between 0.03 and 0.06 mm., so that the combined length of the villi must be considerably in excess, possibly nearly double the figure, 18 kilometers, given above.

#### SUMMARY

The total surface area of the chorionic villi exposed within the placenta described above measured about 7 square meters, of which 6.5 square meters was included in those numerous small branches which by nature of their surface seem suited to act as organs of absorption. The efficiency of these is doubtless further reduced by the numerous thickenings of their epithelium in the form of the masses of nuclei so abundant on the surface of these villi.



Resumen por la autora, Alice L. Brown.

Un simple aparato para la microinyección a mano.

El presente trabajo es una descripción de la construcción y funcionamiento de un aparato de microinyección a mano, basado en un aparato semejante descrito recientemente por Chambers en esta revista. Este aparato, de fácil construcción, puede emplearse para inyecciones en frío o en caliente. Asegura gran delicadeza y libertad de movimientos, de tal modo que los vasos sanguíneos de embriones muy jóvenes pueden fácilmente inyectarse.

Translation by José F. Nonidez  
Cornell Medical College, New York.



## A SIMPLE APPARATUS FOR DELICATE INJECTIONS.

ALICE L. BROWN

*Cornell University Medical College*

### ONE FIGURE

Methods and apparatus for dissecting and injecting cells have been worked upon for a number of years. With the micromanipulator apparatus recently described by Chambers<sup>1</sup> is an injection device consisting of a syringe, a brass tube, and a glass cannula. This device, which is a very simple one, may be easily adapted to injecting the blood vessels of chick embryos or any delicate accurate free-hand injection work under a binocular dissecting microscope. The accompanying illustration shows this device held in a system of ball-and-socket joints which takes the place of the micromanipulator. In addition is a scheme providing for a warm injection mass.

For descriptive purposes this apparatus is divided into three parts:

First, the actual injecting part consists of a syringe<sup>2</sup> (*A*); a hypodermic needle with the tip sealed into one end of a coiled piece of fine extra soft brass tubing<sup>3</sup> (*C*); and into the other end of which (*n*) is sealed a piece of  $\frac{1}{8}$  inch glass tubing (*D*). The glass tube (*D*) is drawn out at one end (*p*) to about 1 mm. inside

<sup>1</sup> Chambers, R. New apparatus and methods for the dissection and injection of living cells. *Anat. Rec.*, vol. 24, 1922.

<sup>2</sup> A 2-c.c. Luer syringe is shown in the figure, but any convenient syringe may be used.

<sup>3</sup> The soft brass tubing used here is one with 2 mm. outside diameter. This or others of somewhat larger sizes may be obtained from any wholesale brass dealer or automobile supply house. If the tubing is too stiff, it may be softened by annealing.

diameter, into which the cannula (*E*) is sealed.<sup>4</sup> The cannula is made by drawing out a glass capillary which will fit into the drawn out end of *D* at *p*. The tip of the cannula is made by momentarily heating the capillary over a microburner and pulling it out just as it softens. This procedure results in a tapering tip which may be broken off to form a pipette of the size which suits the operator. The cannula may be bent at any desired spot to facilitate insertion into the tissue to be injected.

Second, the support for the injecting device in the figure is built out of two Leitz dissecting stands. One complete stand, and the ball-bearing arm, *d'*, of a second, connected together with wooden plugs, as shown in the figure, gives ample freedom for moving the glass tube (*D*) which bears the injecting cannula (*E*). The coils of the brass wire allows the cannula to be moved about while the syringe is held rigid by the clamp, *c'*.

Third, if a warm injection be desired, this is accomplished by arranging a flow of warm water to heat the injection fluid in the glass tube (*D*). This is done by means of a 500-cc. flask (*I*) fastened on the support (*b'*) and a  $\frac{1}{4}$  inch rubber tube connected with it at *j*. The glass tube (*D*) is thrust through the wall of the tubing in two places as indicated in the figure. The lower end of the rubber tube is shunted off to one side of the apparatus and the outflow of the warm water is regulated by the screw clamp (*III*). The water in the flask (*I*) can be heated by an alcohol lamp or a small Bunsen burner and its temperature regulated with the aid of a thermometer. Through the cork (*m*) a small funnel may be inserted for the addition of more water. If a flask with an opening as shown in the figure is not available, a second glass tube must be thrust through the cork of the flask (*I*) to allow the entrance of air. A third tube may be added for the addition of water.

<sup>4</sup> The sealing may be done with ordinary sealing-wax or de Knotinsky cement, which can be obtained from any dealer in chemical and physical apparatus. As the micropipette has to be frequently changed, it must be sealed with a cement which can be readily softened. The de Knotinsky cement is admirable for this purpose.



Resumen por el autor, Morie F. Weymann.

El comienzo y desarrollo de la función en la  
médula suprarrenal de los embriones de cerdo.

Puesto que los experimentos microquímicos y los realizados en tubos de ensayo indican que el precipitado moreno formado cuando se añade epinefrina al bicromato potásico es el mismo material que los gránulos morenos formados en la médula de las glándulas suprarrenales fijadas en soluciones que contienen bicromato potásico, la aparición de gránulos (la reacción cromafínica) en las suprarrenales convenientemente preparadas puede emplearse como un indicador de la presencia de la secreción. Las suprarrenales de los embriones de cerdo, preparadas con este propósito, han sido estudiadas por el autor, quien ha llegado a las siguientes conclusiones: 1) La adquisición de la función secretora comienza gradualmente, comenzando en el estado de 40 a 45 mm. y aumentando hasta el estado de 142 mm., después del cual la reacción permanece sensiblemente constante. 2) Con el comienzo de la función tienen lugar cambios evidentes en el citoplasma y núcleo de las células activas. 3) Algunas células comienzan a presentar la reacción cuando aún están fuera de la corteza y a considerable distancia de su posición definitiva. 4) No todas las células comienzan a funcionar al mismo tiempo. 5) La división celular tiene lugar en ciertas células que presentan una reacción cromafínica definida.

Translation by José F. Nonidez  
Cornell Medical College, New York.



## THE BEGINNING AND DEVELOPMENT OF FUNCTION IN THE SUPRARENAL MEDULLA OF PIG EMBRYOS

MORIE F. WEYMANN

*Department of Anatomy, Washington University School of Medicine*

### FOUR FIGURES

Since the beginning of intensive study of the endocrine glands, these organs have held an important place in the interest of students of growth and differentiation. It has been amply demonstrated that among some of the lower vertebrates endocrine function plays a significant rôle in the regulation of development and metamorphosis, and there are indications that in the mammals it is no less important. In the case of man, it has been suggested that variation in physical type is largely dependent on variation in endocrine activity during growth. What part the glands of internal secretion play in regulating development will probably have to be determined largely by experimentation, but before conclusive experiments can be carried out it will be necessary to have a knowledge of the normal function of the endocrine glands during the embryonic period. A search of the literature shows that a number of attempts have been made to determine whether or not these glands function in the embryo, and that considerable evidence has accumulated on this point. The present work was undertaken with the view of making a study of a single gland in some convenient form in order to determine, if possible, when and how it normally begins to function.

On reviewing what is known of the development of the endocrine glands and considering the feasibility of available tests for function, the suprarenal medulla was selected as best suited for an initial study of this kind. The pig, while not well suited for experimentation, was nevertheless selected because of the abundance of easily available material and the completeness of our knowledge of its development.

Other investigators have commonly relied on biological and chemical tests of the extract from embryonic suprarenals in their attempts to determine the presence or absence of function in these glands. Lewis ('16) states that Moore and Purinton were unable to find evidence of adrenalin in the foetal suprarenals of man by the  $\text{FeCl}_3$  and blood-pressure tests. Svehla ('00) also reported similar results with human material, but he did find adrenalin present in glands from foetal dogs, as did Langlois and Rehns ('99) in those from sheep foetuses. Lewis was unable by chemical and biological tests to demonstrate it in human foetal suprarenals, but by the uterine strip test he got positive indications of its presence in extracts from the suprarenal gland of two full-term still-born infants. Lewis also tried out the color test of Folin and Denis, but concluded that it is useless in the study of foetal suprarenals, because foetal tissues in general are rich in uric acid, which gives the same blue color reaction as epinephrin.

Fenger ('12) found epinephrin by the iodic-acid method in the extract of suprarenals from pig embryos of seventy days; also in that from beef embryos of three months, and sheep embryos of three to four months. McCord ('15) showed, by the uterine-strip method, evidence of epinephrin in the suprarenals of beef embryos as early as the 113-mm. stage. Biological tests could not be carried out on younger embryos because the suprarenals were not large enough to furnish sufficient extract, even when many were used. Langlois and Rehns believed they were able to demonstrate an effect of the suprarenal extract from sixty-day sheep embryos upon the blood pressure of a dog.

Thus it may be seen that there is considerable evidence in the literature that the foetal suprarenals do function, and that they begin to function at an early period. But since there are some possible uncertainties with the biological tests, it seems desirable that the results obtained by them should be checked and supplemented by a thoroughly reliable microchemical test. In the chrome reaction of the medullary cells, discovered by Henle ('65) and interpreted chemically by Ogata and Ogata ('17), we seem to have at our disposal just such a test. Since the time of

Henle it has been known that suprarenals fixed in dichromate solution show a yellow-brown color in the cytoplasm of the medullary cells. This was for a time thought to be a complex adrenalin chromate compound. But the recent work of Ogata and Ogata has furnished convincing evidence that it is a simple inorganic salt, chromium dioxide. It is formed by the reducing action of adrenalin on the dichromate. Kingsbury ('11) has presented evidence pointing in the same direction. He finds that the precipitates formed by various fixing fluids acting on the fresh suprarenal medulla are identical with those produced by the same fluids acting in vitro on adrenalin.

The most critical of the Ogatas' experiments have been repeated and corroborated by the writer. It is found that if commercial adrenalin is added to Müller's fluid in a test-tube, a yellow-brown precipitate slowly forms. Under the microscope it has the same color as is revealed in the cytoplasm of the medullary chromaffin<sup>1</sup> cells after fixation in Müller's fluid. Chemical analysis of this precipitate shows it to be  $\text{CrO}_2$ . As the precipitate is very soluble in alkali, and to a less degree in mineral acids, it was thought advisable to see if these reagents would affect it in the same way in an albuminous solution as in the chromaffin cells themselves. To test this point, a series of sections from a suprarenal gland fixed in Müller's fluid was mounted on slides in the usual way, while on another set of slides was placed a thin

| NO. | TREATMENT                                          | RESULT              |                     |
|-----|----------------------------------------------------|---------------------|---------------------|
|     |                                                    | TISSUE              | PRECIPITATE         |
| 1   | Haematoxylin and eosin stain                       | No change           | No change           |
| 2   | H. and e. stain with ammonia water                 | No change           | No change           |
| 3   | H. and e. with $\text{NH}_4$ and also acid alcohol | No change           | No change           |
| 4   | H. and e. with 2N HCl for 10 min.                  | No change           | Partially dissolved |
| 5   | H. and e. with 2N NaOH for 3 min.                  | Partially dissolved | Partially dissolved |
| 6   | H. and e. with 2N NaOH for 10 min.                 | Partially dissolved | Partially dissolved |
| 7   | H. and e. with 2N NaOH for 15 min.                 | Dissolved           | Dissolved           |

<sup>1</sup> The term chromaffin seems to have been first applied to cells which show the Henle reaction by Kohn ('98).

coating of the precipitate suspended in albumen fixative. The slides were numbered, and one of each set subjected to each of the several treatments indicated in the accompanying table.

Thus it is seen that the precipitate on the slide surrounded by coagulated albumen behaves in much the same manner with regard to solvents as that in the chromaffin cells. The fact that the acid did not affect the granules in the tissue as much as those in the artificial coagulum may very probably be explained by the more intimate relation of the precipitate to the natural protoplasm than to this artificially prepared albumen mixture. These supplementary experiments tend to support the evidence of the Ogatas that the chromaffin substance which appears in the cells is identical with the precipitate that is produced by adrenalin in the test-tube. Therefore the appearance of the Henle reaction in the suprarenal medulla has been considered by the writer as coincident with the appearance of epinephrin in this gland.

Prentiss and Arey's Textbook of Embryology contains the statement that the chrome reaction is an indication of the beginning of function of the gland. The data on which this statement is based are not mentioned in the book, and the writer has not been able to find a specific statement to this effect elsewhere in the literature.

The most satisfactory data with reference to the chrome reaction was found in an article by Wiesel ('01) on the development of the suprarenal medulla. Here it is stated, under his description of a 51-mm. pig, that "die in Chromsalzen geharteten Organe dieses Stadiums geben noch keine chromaffine Reaktion," which would seem to indicate that his next stage, a 63-mm. embryo, showed the brown color. In the description of the 63-mm. size he makes no mention of chrome reaction. If the stage at which Wiesel first found the reaction were at 63 mm., then one might infer that the assumption of function occurs between 51 and 63 mm. But the writer finds that the reaction occurs in stages younger than these. This fact may have been easily overlooked by one not particularly interested in this phase of the problem.

In the series studied here embryos of 218, 142, 85, 75, 65, 55, 45, 40, 30 and 24 mm. were used. Other sizes were studied, but



the above suffice to show the steps in the assumption of function by the suprarenal medulla. There were always several individuals of each size sectioned to check the results, and, when preparing glands from smaller embryos, an older suprarenal of a stage known to show the chrome reaction was always run through in the same container, in order to preclude the possibility of drawing erroneous conclusions on the basis of fortuitous variation in technique. The most satisfactory chrome salt for fixing was found to be the potassium dichromate in Müller's fluid. In the larger embryos the suprarenals were dissected out, the small embryos were sectioned in toto.

The method was as follows: After being fixed in Müller's fluid for two days, the specimens were washed in running water for one hour and then hardened in 70 per cent alcohol for two days more. They were then dehydrated, sectioned by the paraffin method, and stained lightly with neutral haematoxylin and eosin. In the younger stages some were stained only with haematoxylin in the hope of finding fainter chrome reactions, but this did not help as the faintest reaction could be distinguished over a light eosin stain. Washing the specimens for twenty four hours was also tried to see if the precipitate could be washed or dissolved out in that time, but there seemed to be no tendency for this to occur.

In the following account of the suprarenal of the pig at different ages no attempt is made to trace the development of the gland as a whole or to enter into the details of its histology, attention being concentrated on the appearance and development of the chromaffin reaction.

*24-mm. stage.* There is an accumulation of cells, apparently all of the same type, medial to the Wolffian body in the position of the future suprarenal gland. These cells, which are rather polyhedral, with no special cytoplasmic differentiation and round nuclei, have a tendency to be arranged in cords with open spaces between them. Their subsequent history shows them to be cortical cells. There is no evidence of medullary cells in the gland at this time. In the sympathetic ganglion region is a

rather large group of cells which are quite embryonic in type and give no trace of a chromaffin reaction.

*30-mm. stage.* At this stage cells similar in appearance to those in the sympathetic ganglion are seen in the mesenchyme between the site of the suprarenal medulla and the ganglion. There is no brown color in their cytoplasm and the nuclei are rather large and loosely reticular. A few small clumps of these cells appear on the periphery of the suprarenal anlage. The appearance would lead one to suspect migration from the ganglion.

*40-mm. stage.* Beginning with this stage, the suprarenals were dissected out with a liberal amount of surrounding tissues, but the sympathetic ganglion was not included. Cells resembling those of the ganglion extend from its direction toward the gland. Several groups on the periphery of the suprarenal anlage appear to be penetrating between the cortical cells, and there is a difference in structure of the cells in any one group, some tending to become further differentiated as indicated by a decrease in size of the nucleus, which at this time becomes more compact and more deeply staining. There is the faintest suggestion of a chrome reaction, that is, a yellow-brown color, in the cytoplasm of these latter cells.

*45-mm. stage.* In this stage a few of the cells which seem to come from the sympathetic system are inside the cortical mass and numerous groups are on the periphery, with others scattered along toward the sympathetic ganglion region (fig. 1). In the cells with the darker, more deeply staining nuclei there is a faint, but definite, yellow-brown color in the cytoplasm (fig. 2). This color cannot be observed in mesenchymal or renal cells in the neighborhood. Some of these chromaffin cells are found in groups which are at some distance from the cortical anlage in the direction of the sympathetic ganglion. As these clumps of cells increase in size and as mitotic figures (fig. 3) are seen among them, the assumption is justified that they are multiplying as well as maturing.

*55-mm. stage.* Groups of medullary cells are evident in the periphery and toward the center of the cortical mass. About half of the medullary cells show the yellow-brown chrome re-

action, which is of a somewhat deeper color than in those of the 45-mm. stage. The color also varies in the individual cells within a group, being apparently deeper in those which, judged by their nuclei, are most differentiated.

*60 mm. stage.* There is little change from the 55-mm. stage except that the chrome reaction is more marked and more general, and some groups of medullary cells are situated more deeply in the cortical mass.

*65-mm. stage.* The reaction is present in the majority of medullary cells. Islands of these latter are scattered throughout the cortex. The relative amount of medulla is less than in later stages. Mitotic figures are seen in certain chromaffin cells.

*75-mm. stage.* Chromaffin cells are for the most part in the middle portion of the gland cortex, with some peripheral and some central. The reaction is more marked, and is now of about the same intensity in all the medullary cells.

*85-mm. stage.* In this stage the medulla is not yet entirely central. All medullary cells show a definite chromaffin reaction, but the maximum intensity has not yet been reached. Those on the periphery are as dark as those which are central in position. The nuclei of the chromaffin cells are not so dense as in the earlier stages, but do not have the loose network characteristic of the primitive undifferentiated cells of stages before the first appearance of the chromaffin reaction.

*142-mm. stage.* All medullary cells are central except one group seen on the periphery of the gland and a few strands running into the cortex. The intensity of the reaction in the individual cell has now reached its maximum (fig. 4) and is not darker in older stages.

*218-mm. stage.* Chromaffin cells are all centrally placed constituting a typical suprarenal medulla. The density of color is the same as in the 142-mm. stage. The individual cells have fairly abundant cytoplasm with rather dark-staining granules and spherical or oval nuclei. Many of the nuclei appear to have a brown tint, but careful study of the preparations shows that when this appearance is observed it is to be attributed wholly to

the brown granules in the overlying cytoplasm. The cortical and tissue cells show no brown color in the cytoplasm.

The observations recorded in the preceding descriptions may now be recapitulated in a few paragraphs which, it may be recalled, refer only to suprarenals of pig embryos that have been treated according to the technique indicated at the beginning of this paper.

1. The earliest indication of the chromaffin reaction that can be detected appears in embryos of about 40 mm. In embryos of 45 mm. the reaction has become very definite, from which fact it appears that it is at about this time that medullary cells begin to produce, or at least to store, adrenalin.

2. In early stages the reaction is observed in cells which are not at the site of the future suprarenal gland. This observation presents no difficulty if one accept the view that the medullary cells reach their definitive position by migration from the sympathetic—a view which is clearly set forth by Whitehead ('02) and by Wiesel, who states that there is no longer any doubt that the suprarenal medulla "stammt einzig und allein vom Sympaticus und dessen Ganglien" (loc. cit., p. 141).

3. Assumption of the ability to give the chromaffin reaction occurs concomitantly with modification in the histological appearance of the cell, involving changes in the size and staining reaction of the nuclei. The suspicion might have arisen that these changes, including the chromaffin reaction, indicate degeneration of certain cells in each group, but no evidence was found that such is really the case.

4. Since cells that show the reaction are found in process of mitosis, it is clear that the function begins in a relatively undifferentiated condition of the cells, which are both multiplying and specializing as they approach their definitive position.

5. The fact that in the intermediate stages cells in the medullary region and those at the periphery of the cortex may show the same color intensity gives further evidence that the function of a cell is not wholly dependent on its position. The more mature cells, as indicated by the chromaffin reaction, are not necessarily the first to reach their destination.



6. The assumption of the function which is indicated by a chromaffin reaction takes place gradually in the medullary cells of embryos from 40 mm. to 75 mm. in length. After the latter stage apparently all the medullary cells show the reaction. Its intensity in individual cells increases from the 40-mm. to the 142-mm. stage.

In summary, the development of function by the medullary cells of the suprarenal gland may be briefly stated as follows: The groups of embryonic cells found in the 24-mm. embryo between the sympathetic ganglia and the anlage of the suprarenal cortex give no indication of specific function. At between 40 and 45 mm. certain of them begin to show a faint chromaffin reaction in their cytoplasm, their nuclei at the same time becoming denser, smaller, and more deeply staining. As the embryo grows these medullary cell groups penetrate the cortical anlage and finally occupy its central portion at the 142-mm. stage. During this process mitosis continues, all the cells gradually assume the capacity for a darker constant chromaffin reaction, the relative amount of cytoplasm increases, and the cells become from one and one-half to two times their original size. The nuclei are no longer as dense as when the cells first began to exhibit the chromaffin reaction, but are smaller, darker, and more granular than in the undifferentiated cell.

These findings tend to confirm and supplement the results, so far as they go, of other workers who have used different methods and material. They fix more closely than has been done before the time at which one of the mammalian endocrine glands begins to function in a definite manner, and show that not all the medullary cells of the suprarenal gland begin their activity at the same time or in the same place. Of especial interest is the indication that the functioning of the medullary cells is dependent upon some intrinsic factor in the cell itself rather than upon its position with reference to other tissues. Since no evidence of medullary function was found in embryos under 40 mm., at which time the principal organs and systems are well established, it does not seem probable that any primary

malformations can be traced to disturbances in the epinephrin production of the embryo itself.

The writer is indebted to Dr. C. H. Danforth for suggesting the problem and for criticism of the work.

#### LITERATURE CITED

- FENGER, F. 1912 On the presence of active principles in the thyroid and suprarenal glands before and after birth. *Jour. Biol. Chem.*, vol. 11, pp. 489-492.
- HENLE, J. 1865 Über das Gewebe der Nebenniere und der Hypophyse. *Zeitschr. f. rationelle Med.*, Bd. 24, S. 143-152.
- KINGSBURY, B. F. 1911 The term 'chromaffin system' and the nature of the 'chromaffin reaction.' *Anat. Rec.*, vol. 5, pp. 12-16.
- KOHN, ALFRED 1898 Ueber die Nebenniere. *Prag. med. Wochenschr.*, Jahrg. 23, S. 193-195.
- LANGLOIS, J. P., AND REHNS, J. 1899. Les capsules surrénales pendant la période foetale. *Compt. Rend. Soc. Biol.*, T. 51, pp. 146-147.
- LEWIS, J. H. 1916 The presence of epinephrin in human foetal adrenals. *Jour. Biol. Chem.*, vol. 24, pp. 249-254.
- MCCORD, C. P. 1915 The occurrence of pituitrin and epinephrin in foetal pituitary and suprarenal glands. *Jour. Biol. Chem.*, vol. 33, pp. 435-438.
- OGATA, T., AND OGATA, A. 1917 Henle's reaction of the chromaffin cells in the adrenals and the microscopic test for adrenalin. *Jour. Exper. Med.*, vol. 25, pp. 807-817.
- SVEHLA, K. 1900 Experimentelle Beiträge zur Kenntniss der innern Secretion des Thymus, der Schilddrüse und der Nebennieren von Embryonen und Kindern. *Arch. Exp. Path. u. Pharm.*, Bd. 53, S. 321-341.
- WHITEHEAD, R. H. 1902 The histogenesis of the adrenal in the pig. *Am. Jour. Anat.*, vol. 2, pp. 349-360.
- WIESEL, J. 1901 Über die Entwicklung der Nebenniere des Schweines, besonders der Marksubstanz. *Anat. Hefte*, Bd. 16, S. 117-148.

PLATES

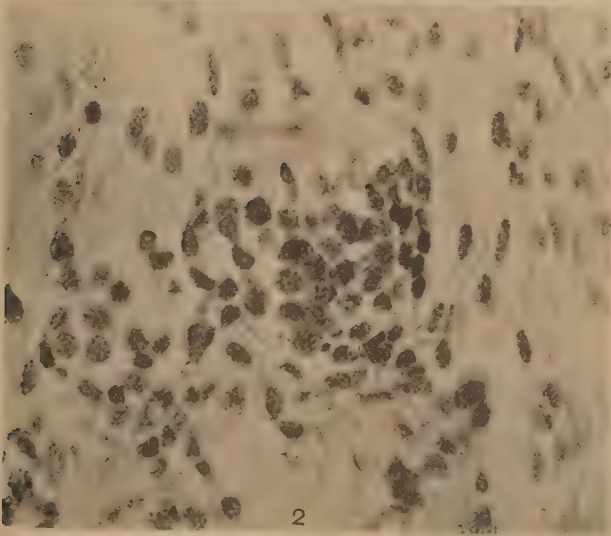
## PLATE I

### EXPLANATION OF FIGURES

1 Section of the suprarenal gland from a 45-mm. pig embryo fixed in Müller's fluid and stained with neutral haematoxylin and eosin. Magnified about  $\times 40$ . The specimen shows, to the right, strands of chromaffin cells at and near the hilus and to the left the cortical part of the gland. The square indicates the region shown in figure 2, the circle that shown in figure 3.

2 Higher magnification of the region marked by a square in figure 1. The darker cells with small dense nuclei are the ones in which the chrome reaction is first definitely evident. The embryonic character of the other cells may be noted. This group of cells while near the cortex is not surrounded by it. Magnification about  $\times 700$ .



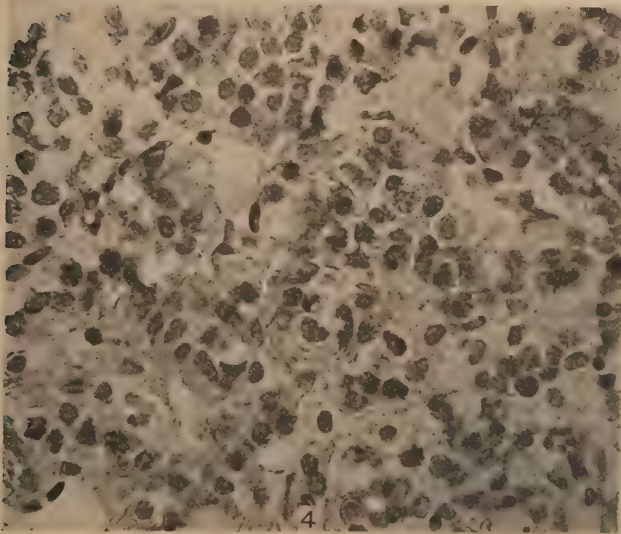
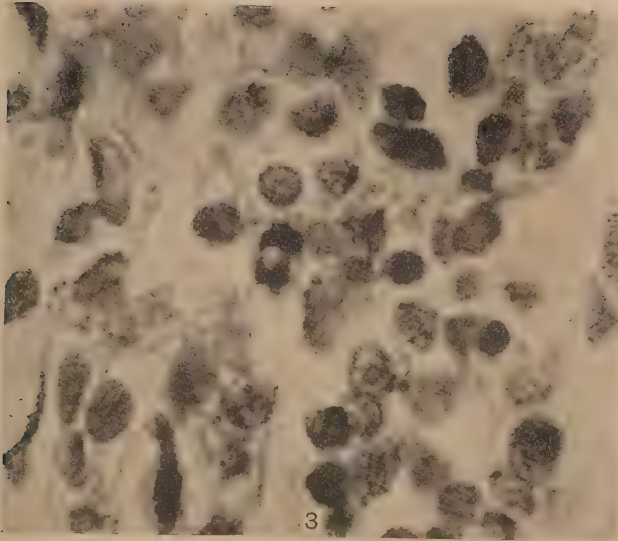


## PLATE 2

### EXPLANATION OF FIGURES

3 Area within the circle marked on figure 1, selected to show mitosis in a cell which already exhibits the chromaffin reaction. Magnification about  $\times 960$ .

4 A region of the suprarenal gland of a 142-mm. pig embryo fixed in Müller's fluid and stained with neutral haematoxylin and eosin. In this section the medullary cells show the chromaffin reaction at its height. The granules in the cytoplasm are of a yellowish brown color. Magnification about  $\times 700$ .



Resumen por los autores, H. B. Goodrich y J. A. Scott.

El efecto de la luz sobre los cultivos de tejidos.

El presente trabajo describe los resultados de experimentos llevados a cabo con el fin de comprobar el crecimiento relativo de los cultivos de tejidos a la luz y en la oscuridad. El material empleado ha consistido en trozos del corazón del embrión de pollo. Los autores han empleado una luz más intensa que la usada ordinariamente para las observaciones microscópicas o que la empleada para calentar las incubadoras. Los resultados obtenidos indican que los tejidos durante el crecimiento inicial desde el trozo cultivado prosperan del mismo modo en la luz que en la oscuridad. Los autores describen el aparato empleado para incubar los tejidos a iguales temperaturas a la luz y en la oscuridad.

Translation by José F. Nonidez  
Cornell Medical College, New York.



## THE EFFECT OF LIGHT ON TISSUE CULTURES

H. B. GOODRICH AND J. A. SCOTT

*The Biological Laboratory of Wesleyan University*

### ONE FIGURE

The following experiments were designed to test the effects of ordinary types of illumination on tissue cultures. In the course of other work with tissue cultures, the question had arisen as to whether the method of heating an incubator with an electric-light bulb would prove harmful. Also C. C. Macklin ('16) has reported that ordinary illumination for microscopic observation caused degeneration of cultures, while on the other hand S. J. Holmes ('14) has stated that "Light has very little effect on epithelial cells in tissue cultures."

The incubator used was one which had been made in the University workshops and which is heated by electric resistance wires giving no light. It was necessary to have a control series of cultures kept in the dark at the same temperature as those exposed to light. The apparatus used to maintain these conditions for the two sets of cultures is illustrated in figure 1, and consisted of the following parts. Two cubical tin cracker boxes having hinged doors and measuring about 10 inches on a side were placed on the upper shelf of the incubator. One of these was the dark box (*H*) and the other the light box (*I*). Light was admitted to the incubator and the light box through windows. The source of light was a 600-watt electric lamp, with tungsten filament, filled with inert gases, and commercially known as Mazda, type C, stereopticon tubular bulb, style T, 20. This was placed (at *A*) in a stereopticon; the projection lenses were removed, but the condensing lenses (*B*) retained. The light passed through the condensing lenses and next through the circulating water-bath (*C*), which was originally a part of another projection apparatus. The light was then reflected by a mirror

(*D*) placed at an angle of  $45^{\circ}$  to the vertical, and passed successively through the projection lenses (*E*) of the stereopticon, a crystallization dish containing water (*F*), a window in the roof of the incubator, a window in the light box closed by a glass plate (*G*), and then on to the tissue cultures placed on a shelf in the light box.

This method proved adequate for the removal of all heat radiation, and thus the temperature of the two boxes remained very nearly equal. About five observations of temperature were made each day for both light and dark boxes. Usually the same temperature was noted in both readings, and there was seldom a difference greater than  $1^{\circ}$  C. Temperatures were maintained within the usual range for chick tissue incubation— $37$  to  $39^{\circ}$  C.

The light reaching the cultures was measured by a luxometer which had been previously calibrated by the United States Bureau of Standards. The measurements showed a light intensity of about 270 foot-candles with a possible error of 20 per cent. This is about equal to the light yielded by a tungsten bulb of 200 watts placed 10 inches from the illuminated surface, and thus is greatly in excess of light from bulbs used as a source of heat in incubators. Further, this intensity of light was compared with that used in ordinary microscopic illumination. The amount of light from a microscope lamp with 'Daylite' glass placed immediately in front of the microscope mirror and with diaphragm open wide was compared with a light of known intensity.<sup>1</sup> It proved to yield 158 foot candles. This was a greater intensity of light than that which had ordinarily been used in the observation of cultures, as the lower diaphragm was usually partially closed. It was, however, considerably less than the maximum illumination obtainable by placing the light directly under the microscope and with the diaphragm wide open. This was measured to give 1099 foot-candles.

Cultures were made of heart tissue of chick embryos of from seven to fifteen days' incubation, and these were planted in the usual manner in hanging drops on the under surface of cover-slips sealed over depression slides. Two media were used: in

six experiments the blood plasma of the fowl, and in three experiments the sea-water and chicken bouillon as used by M. R. Lewis ('14). Tissue from the same heart was used in each ex-

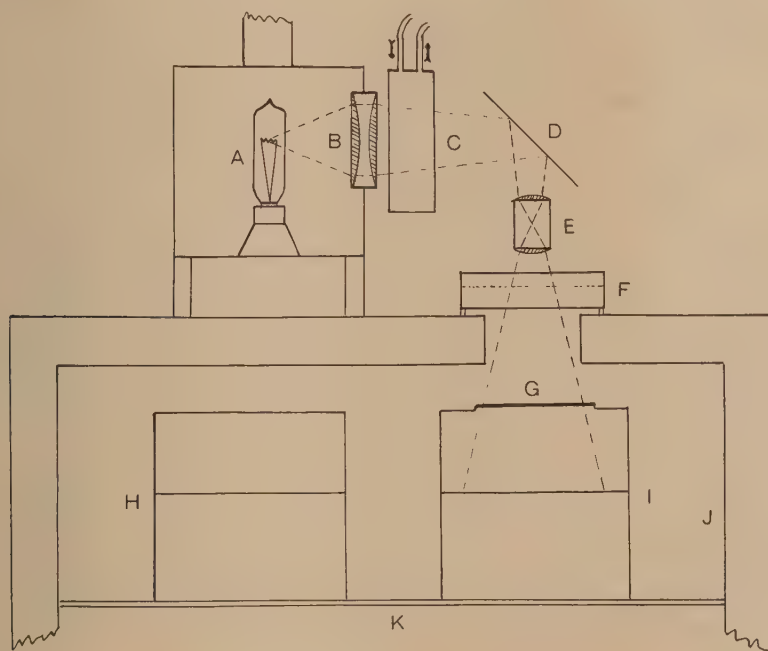


Fig. 1 Apparatus for incubating tissues at equal temperatures in light and dark. *A*, electric lamp; *B*, condensing lenses; *C*, circulating water-bath; *D*, mirror; *E*, projecting lenses; *F*, water-bath; *G*, glass window; *H*, dark box with shelf for cultures; *I*, similar light box; *J*, wall of incubator; *K*, shelf of incubator.

periment for both sets of cultures. Usually not more than eight or ten cultures could be placed in the lighted area. The results of one experiment, as an example, and the total of all experiments are shown in tables 1 and 2, respectively. The designation of slight, moderate, and abundant growth is arbitrary. The term growth is used as has been the practice in tissue-culture work to

indicate the migration of cells from the explant without definite knowledge of the amount of cell division involved. 'Slight' growth indicates a condition where only a few isolated strands of cells were observed. 'Moderate' growth means a condition of growth more vigorous than slight growth up to a condition such that the explant is surrounded by cells extending a distance about equal to one-half of its diameter. And finally, 'abundant' growth signifies further spreading, which was seldom greater than a distance equal to the diameter of the explant. The observations of the conditions of the cultures were made up to five days after planting, by which time the active wandering of cells had usually ceased in all cultures. The average period of growth upon which observations in the tables are based was four days. Muscular contractions were frequently noted in both series of cultures. In a few cases stained preparations showed mitotic figures in wandering cells. These were noted in both types of cultures, but were so infrequent as to render comparative data of little value.

It will be noted from these tables that growth in the light box was practically as good as that in the dark box, and the variation probably lies within the range of variation due to other causes. There are certain probable causes of variation in tissue cultures which are difficult to obviate. These are variations in size of drop of medium, in size of the explant, in period of evaporation of medium during process of mounting.

These experiments seem clearly to indicate that polychromatic light from an incandescent electric bulb of not over 270 foot-candles has no deleterious effect in the initial growth of tissue cultures from the heart of the chick embryo. Thus the illumination used in incubators and in ordinary microscopic observations is harmless.

#### BIBLIOGRAPHY

- HOLMES, S. J. 1914 Behavior of the epidermis of amphibians in cultures. *Jour. Exp. Zool.*, vol. 17.
- LEWIS, M. R. 1916 Sea water as a medium for tissue cultures. *Anat. Rec.*, vol. 10, no. 4.
- MACKLIN, C. C. 1916 Binucleate cells in tissue cultures. *Carnegie Institution, Contributions to Embryology* no. 13. Publication 226.



TABLE 1

*Experiment started May 7, 1921. Cultures grown for five days*

|          | NO GROWTH | SLIGHT GROWTH | MODERATE GROWTH | ABUNDANT GROWTH |
|----------|-----------|---------------|-----------------|-----------------|
| In light | 2         | 0             | 4               | 4               |
| In dark  | 1         | 0             | 7               | 2               |

TABLE 2

*Summary of all experiments*

|          | NO GROWTH | SLIGHT GROWTH | MODERATE GROWTH | ABUNDANT GROWTH | TOTAL |
|----------|-----------|---------------|-----------------|-----------------|-------|
| In light | 14        | 11            | 19              | 24              | 68    |
| In dark  | 14        | 15            | 19              | 16              | 64    |

<sup>1</sup> Estimate of light intensity was made by comparison with light of known power by the greased-spot method. A light of 247 candle-power gave at a distance of 15 inches illumination equal to that from the microscope lamp focused by a condenser at the position of a microscope slide. The following formula was used for conversion into foot-candles:  $\frac{c \sin \phi}{d^2}$ .  $c$  is the known

candle power,  $\phi$  the angle between light rays and surface, in this case  $90^\circ$ , and the  $\sin$  is 1.  $d$  is the distance in feet from the illuminated surface. By substitutions the formula then reads:  $\frac{247 \times 1}{(\frac{5}{4})^2} = 158$ .

Resumen por el autor, A. B. Dawson.

El origen y presencia de una sola arteria umbilical  
en los fetos humanos normales y anormales.

En la literatura se han descrito dos grupos de arterias umbilicales impares. En el primer grupo se incluyen aquellas que se originan en la aorta; en el segundo las que se originan en el tronco de la iliaco-hipogástrica común. En el presente trabajo se describen dos casos representativos de estos dos grupos. El perteneciente al grupo primero fué hallado en un mónstruo simpódico, el otro aparecía en un feto hembra formado normalmente. Las arterias umbilicales impares que se originan en la aorta están generalmente asociadas con la condición simpódica. Algunas veces en fetos simpódicos las dos arterias umbilicales permanecen casi por completo separadas. En otros casos solamente se pierde la porción distal de uno de los miembros del par umbilical. La llamada fusión de las arterias umbilicales para formar un solo vaso medial no puede, por esta causa, considerarse como la causa de la condición simpódica. El autor da una lista de los factores que entran en la formación de las arterias umbilicales variantes. El factor que produce la predisposición a la formación de arterias umbilicales impares que aparecen como ramas aórticas directas es la persistencia de las raíces umbilicales ventrales. Las arterias umbilicales impares que se originan en la aorta en un nivel alto y pasan directamente al ombligo, han sido interpretadas por muchos como arterias onfalomesentéricas persistentes. Estos vasos representan más probablemente arterias umbilicales primarias fusionadas. Las arterias umbilicales impares laterales que se originan en el tronco común iliaco-hipogástrico se han desarrollado normalmente. La ausencia de una arteria umbilical en el lado opuesto se debe a la atrofia de su porción distal después del establecimiento de su raíz dorsal o a la ausencia de la raíz umbilical primaria.

## THE ORIGIN AND OCCURRENCE OF THE SINGLE UMBILICAL ARTERY IN NORMAL AND ABNORMAL HUMAN FETUSES

ALDEN B. DAWSON

*Loyola University School of Medicine, Department of Anatomy*

NINE TEXT FIGURES

### INTRODUCTION

The single umbilical arteries described in the literature can be divided into two groups. Group 1 includes all which arise from the abdominal aorta, whether as direct branches or as caudal continuations of the vessel itself; group 2, those which take origin from either the right or left common iliac-hypogastric trunk. Recently two cases of the occurrence of a single umbilical artery in full-term fetuses have come under my notice. These were representative of the two groups just mentioned. In one specimen (Dawson, '22), a symphyodial monster, the single median umbilical artery arose directly from the aorta a short distance below the superior mesenteric artery (fig. 2). In the other, a normally formed fetus, only the left umbilical, appearing as a branch of the hypogastric artery, was present (fig. 1). These two cases, together with a rather extensive survey of the literature, form the basis of this paper.

A single umbilical artery is an almost constant feature of the fetal monstrosity symphodia, and the constancy with which it appears in this class of monster has led many to conclude that the single median umbilical artery is the primary anomaly and that the other concomitant anomalies are subsidiary to it. Johnston ('20) is probably the latest exponent of this theory. Ballantyne ('04), too, after a comprehensive survey of human monstrosities, pointed out that fetuses in which there is only one umbilical artery are generally malformed, and those in which the

single artery is mesial in position and arises directly from the aorta are nearly always malformed in one special way, namely, exhibit fusion of the lower limbs or sympodia. He, with many others, believed, furthermore, that the single median artery supplying the cord was vitelline in origin, being the persistent omphalomesenteric artery, and concluded like them that the arterial supply of the placenta was not an allantoic derivative. The latest writer to express this view of the vitelline origin of the single umbilical artery is Taglicht ('21).

Why there should be normally two umbilical arteries and only a single vein in the fetal cord is not clear. The venous supply of the placenta is primarily bilateral, but the median umbilical vein of fetal life is the persistent left umbilical of the embryo, the right having atrophied during early embryonic development. Furthermore, in the development of the vascular system of the higher vertebrates there is to be noted a general tendency for primitive bilateral vessels to be transformed secondarily into single, and sometimes median trunks. This is especially true if the vessels supply organs which, like the cord and placenta, are not bilateral.

In many cases it is difficult to determine the manner in which the transformation into a single vessel is effected. In some vessels it is evident that one member of the pair gained the ascendancy and its fellow atrophied consequently. In other cases the two vessels were probably completely fused to form a single trunk. Apparently, single umbilical arteries may be derived in either way, but the courses and relations of the single blood vessels are by no means identical. Moreover, the manner in which a single umbilical artery may be derived is also greatly complicated by several features of the normal development of these vessels. The primary umbilical arteries which rise ventrally from the abdominal aorta normally migrate from the cervical to the lumbar region. In the latter position (fig. 3) they acquire secondary connections with dorsolateral branches of the aorta, and following the establishment of these dorsal relations the primary or ventral connections with the aorta atrophy.



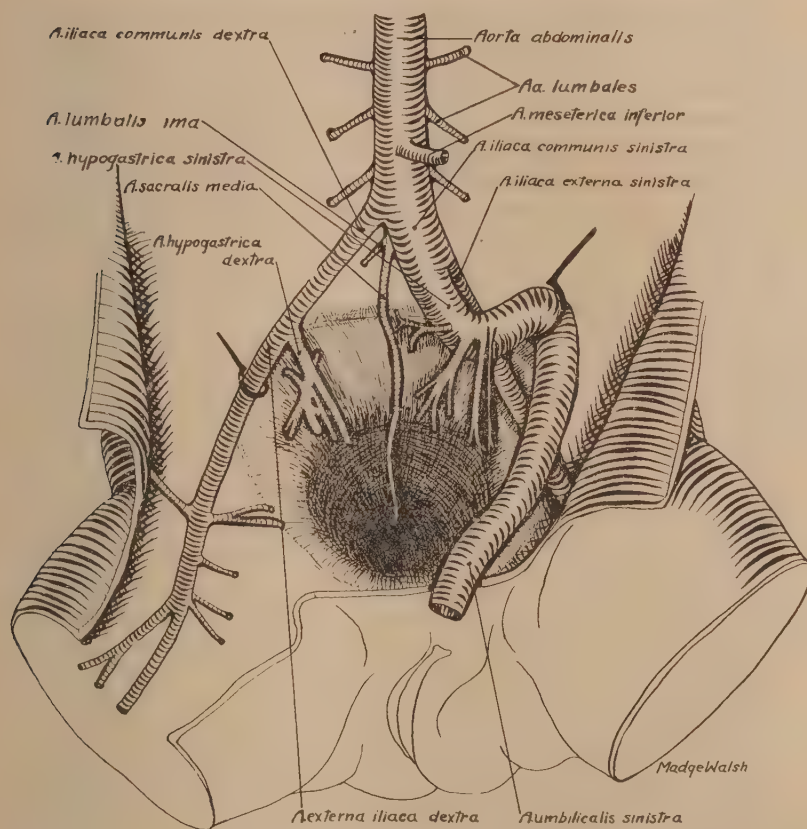


Fig. 1 Ventral view of the pelvis of a female fetus, showing the absence of the right umbilical artery. The relations of the right external iliac and the left umbilical arteries have been disturbed to display the smaller vessels distributed to the pelvic region. For complete description see text.

The substitution of dorsal roots for ventral roots may possibly explain why a single umbilical artery is not more commonly encountered in normal development. The dorsal segmental pairs of vessels are never, in human embryos, converted second-

arily into single arteries, while the ventral vitelline series normally undergoes this transformation, and the umbilical or allantoic arteries are regarded as caudal members of the vitelline series. In cases, therefore, in which the dorsal connections are never established or if established fail to persist (and the primary ventral roots are accordingly maintained), it would be expected that the umbilical arteries would exhibit a tendency to duplicate the history of their homologous series, the paired vitelline arteries, and would be accordingly converted into single trunks. These single trunks would also necessarily arise directly from the abdominal aorta, and not from the common iliac-hypogastric trunk as they do if the normal plan of development is followed. Other cases, in which the single umbilical artery arises from either the right or left hypogastric, admit of another explanation. This will be discussed later.

From the preceding statements it will be evident that there is not, as yet, complete agreement regarding the origin and occurrence of the single umbilical artery in man, and in this regard I wish to present, in the succeeding pages, evidence in support of the following conclusions: 1) that a single umbilical artery, arising directly from the aorta, is not the primary anomaly in sympodial monsters; 2) that the development of such a blood vessel is probably favored by the persistence of the original ventral umbilical roots; 3) that in order to satisfy the facts it is not necessary, except in rare cases (Ballantyne, '98), to interpret the single umbilical arteries belonging to group 1 as persistent omphalomesenteric arteries, and, 4) that single arteries of group 2 are the result either of the failure of one member of the umbilical pair to develop originally or of the secondary atrophy of the distal as well as the proximal portion of a primary artery on either the right or left side following the establishment of its dorsal connections. The latter of the alternative explanations seems the more probable one, although little direct evidence can be produced to substantiate it.

I wish to acknowledge my indebtedness to Dr. H. D. Senior for many helpful criticisms and suggestions. He is, however, in no way responsible for any of the conclusions drawn in this paper.

## A SINGLE UMBILICAL ARTERY IN A NORMALLY DEVELOPED FETUS

The subject of this description was a full-term female fetus used for dissection in a course in fetal anatomy. Interest in the condition of the umbilical arteries was aroused on observing a great difference in the size of the right and left common iliac arteries (fig. 1), the left being several times larger than the right. A careful search failed to reveal even a trace of a right umbilical artery. The right hypogastric and the right external iliac arteries, however, were normal in size and position. The right ovarian was abnormal and has already been described (Dawson and Reis, '22). The right superior vesical artery was also lacking. Four paired lumbar arteries were present, and on the right side an *a. lumbalis ima* was found.

The arrangement of the arteries from the left hypogastric conformed to what Piersol ('07) has designated fetal type II (p. 810, fig. 725), in which the three large vessels, the superior gluteal, the internal pudendal, and the inferior gluteal arise independently from the main (hypogastric) trunk (McMurrich, '20, p. 248, fig. 154). The single umbilical artery had practically the same caliber as the abdominal aorta.

## A SINGLE UMBILICAL ARTERY IN A SYMPODIAL MONSTER

The main features of the anatomy of this monster have already been briefly reported (Dawson, '22). The umbilical artery was single and approximately median. It arose from the abdominal aorta a short distance below the superior mesenteric artery (fig. 2). Below the point of origin of the umbilical artery the dorsal aorta was greatly diminished in size and gave off inferiorly only the lumbar arteries, second, third, and fourth right, and second and third left. It terminated in a small vessel suggestive of a middle sacral artery and did not have any further connection with the arterial supply of the pelvis and lower extremities.

The umbilical artery, on the other hand, was very large, equaling in size the vessel from which it arose. In the upper portion of the abdominal cavity it occupied a position slightly ventral

and lateral (left) to the dorsal aorta and was enclosed in a low peritoneal fold. More caudally, this fold was materially increased in height and in the pelvic region formed a sickle-shaped septum which partitioned the rudimentary pelvic cavity into right and left halves. The umbilical artery which was located in the free margin of this fold accordingly curved ventrally in the sacral region and then ascended toward the umbilicus on the anterior abdominal wall in the midventral line. The artery was displaced slightly to the left by the descending colon, which was distended with meconium, as the rectum and anus were absent. This displacement is somewhat exaggerated in figure 2 to show the courses and relations of the dorsal blood vessels.

Shortly after its origin from the aorta, the umbilical artery gave off an apparently normal inferior mesenteric artery, and in the sacral region a second and very prominent branch was found. It arose as a median dorsal trunk at the point of greatest convexity of the umbilical artery as it curved forward and upward to supply the umbilical cord. This dorsal branch was 1.5 cm. long and bifurcated in the shallow pelvis, giving rise to two large lateral vessels which, after giving off a few small arteries to supply the pelvis, continued into the 'fused' lower limbs.

#### A SCHEMATIC OUTLINE OF THE VARIOUS FACTORS INVOLVED IN THE FORMATION OF VARIANT UMBILICAL ARTERIES

The scheme, outlined below, is based primarily upon the normal ontogenetic plan of the umbilical arteries (Felix, '10; Hochstetter, '90; Senior, '19; Tandler, '03), but it is, in parts, supplemented by a study of two dissections I have made and by analyses of the many umbilical variants reported in the literature. The factors are as follows:

1. The failure of one member of the primary pair of umbilical arteries to develop.

2. Variations in the caudal migration of the umbilical arteries from the cervical to the lumbar region: *a*) arrested migration, the arteries arising from the aorta at a low thoracic or high lumbar level (fig. 4); *b*) complete or normal migration (fig. 3).



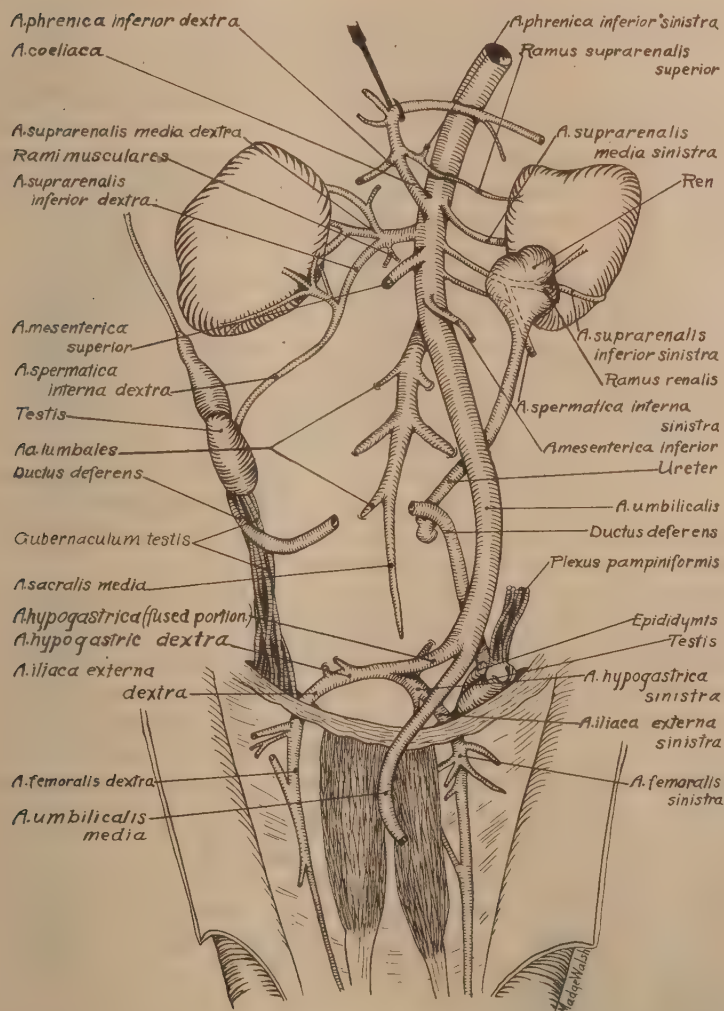


Fig. 2 Ventral view of the abdominal region of a symphyliac monster, showing the anomalous arterial supply and the rudimentary urinogenital system. For description see text.

(There may also possibly be cases of normal migration followed by return, thus simulating arrested migration.)

3. Variations in the development of dorsal or secondary roots: *a*) failure of the dorsal roots to connect with the umbilical arteries (fig. 4), dependent to some extent on 2*a*; *b*) normal dorsal root connections established with the primary paired umbilical arteries; *c*) unilateral development of the dorsal roots, in cases where both primary arteries are present or where only one member of the primary pair is present.

4. The varying fates of the primary (ventral) and the secondary (dorsal) roots in the condition 3*b* or 3*c*: *a*) loss of both primary roots and the persistence of the dorsal root or roots (normal); *b*) the persistence of both dorsal and ventral roots more or less completely; *c*) loss of the proximal portions (i.e., proximal to the point of origin of the primitive external iliac artery) of the dorsal roots and the persistence of the ventral roots; *d*) the loss of one dorsal and one ventral root; *e*) the persistence of two dorsal roots and one ventral root; *f*) the loss of one dorsal root and the persistence of two ventral roots.

5. The method of transformation of the paired umbilical arteries into a single vessel. (Although in many cases there is no direct evidence to indicate that the single umbilical arteries are derived from primitively paired vessels, still the fact that two dorsolateral connections were made has been accepted as indirect evidence of such a condition, since it hardly seems possible for a single median branch of the aorta to establish these connections.) *a*) By the loss of one umbilical artery distal to the point of origin of the external iliac artery. (It must be kept in mind, however, that the point of origin of the external iliac artery is not an absolutely fixed one, since this artery may also migrate either proximally or distally along the common iliac-hypogastric trunk.) *b*) By the fusion of the two umbilical arteries, influenced possibly by conditions represented in 2*a*, 3*a*, and 4*b*, 4*c*, or 4*f* (fig. 5).

6. The varying fates of the lumbar and sacral portions of the abdominal aorta. The lumbar portion, *a*) persists in condition 3*a* and 4*a*, but, *b*) usually undergoes more or less atrophy caudal

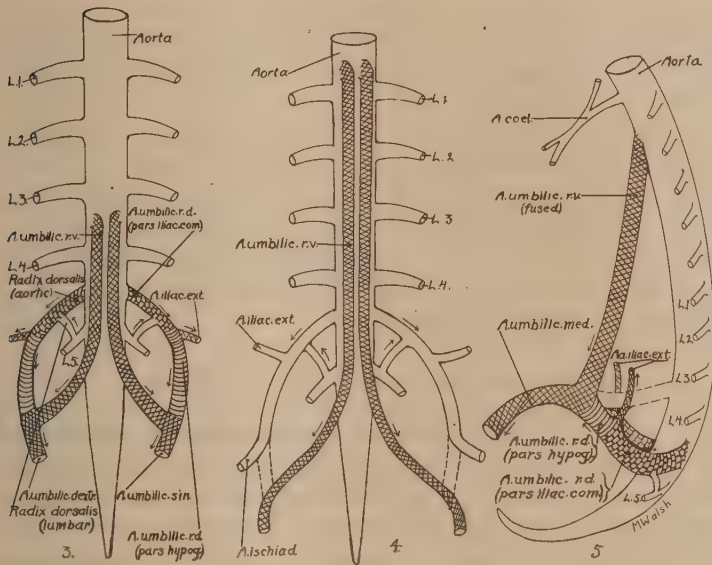


Fig. 3 Diagrammatic representation, ventral view, of the developing abdominal aorta, showing the normal development of the arteries of the lower limbs and umbilical cord. Both dorsal and ventral roots of the umbilical arteries are indicated. The several portions of the arterial system of special interest in this paper are distinguished by hatching and stipple, and this method is adhered to uniformly in all subsequent figures (4 to 9). *r.v.*, radix ventralis; *r.d.*, radix dorsalis. The other abbreviations do not need explanation. Arrows indicate the direction of blood flow.

Fig. 4 Diagrammatic representation, ventral view, of the developing abdominal aorta, illustrating a condition in which the ventral umbilical arteries have failed to complete caudal migration and to establish secondary connections (dorsal roots) with the aorta.

Fig. 5 Diagram showing abnormal development of the abdominal aorta as seen from the left side. The ventral umbilical arteries have failed to migrate caudally and have fused to form a single median vessel. They have also established dorsal root connections with the aorta. The normal position of the ventral umbilical roots is shown by broken lines.

to the point of origin of the ventral umbilical roots in a condition represented by 2a and 5b or 4c. The sacral portion is, c) often missing, especially in sympodial monsters but, d) may persist.

7. The possibility of a single umbilical artery or any other large single trunk, which arises from the aorta at the lower lumbar level to become terminal in position. The normal middle sacral is rarely terminal.

8. The possibility in cases where the original ventral roots are fused and the dorsal roots atrophy proximally, *a*) for the distal or persistent (hypogastric) portions of the dorsal roots to be transformed (apparently by fusion) into a single trunk which would accordingly take its origin from the dorsal aspect of the single umbilical artery. This fusion, however, *b*) may be incomplete or, *c*) may not occur at all.

#### REVIEW OF LITERATURE AND DISCUSSION

The review of the literature has been postponed until this time and the somewhat hypothetical explanation of single umbilical arteries interpolated between it and the description of the two dissections in order that the two cases described and the several cases reviewed might be utilized as cumulative evidence in support of the conclusions noted above. The discussion, it is hoped, will also be facilitated by having before us in a schematic form a list of the various factors which may possibly be effective in the formation of variant umbilical arteries. These factors will be referred to by the number and letter under which they are listed. No attempt will be made to review the literature completely. Only cases which are believed to have a direct bearing on the points under consideration have been selected.

A single median umbilical artery in direct continuity with the abdominal aorta has long been regarded as a constant feature of sympodia and its importance has been, I believe, to a large extent over-emphasized. Johnston ('20) and many earlier writers regarded the single vessel as the primary anomaly. They believed that it was not the persistent member of a pair, but was formed by the 'fusion' of the two umbilical arteries, and that it therefore acted both mechanically, by forming an obstruction to caudal development, and physiologically, by resulting in a deficiency in the vascular supply to the posterior end of the body.



(The word 'fusion' has been rather loosely used in the literature with little or no indication as to whether 'failure to develop separately' or 'secondary union following separate development' was meant. Unless it is indicated otherwise, as above, by means of quotation marks, the latter meaning is implied when the term is used here.)

If Johnston's suggestion, that the formation of a single median umbilical artery is the primary anomaly in sympodia and is directly responsible for the defective development of the caudal portion of the body, is correct, it would follow that in all cases of sympodia that there must always be but one artery and it must also be median in position. In reviewing the literature, however, it is obvious that the single umbilical artery in sympodial monsters is not always formed by 'fusion,' but is in some cases without question a persistent member of a pair of vessels. As early as 1889 Schwing demonstrated a case of symplus dipus in which "*Der Nabelstrang enthält nur eine Nabelarterie welche aus der linken A. iliaca entspringt*" (p. 485). This is apparently an ordinary case of unilateral persistence, with a secondary (dorsal) root, of one member of the umbilical pair. Later Odisio ('92) figured and described the abdominal arterial supply of a case of sirenomelus, in which it is evident that the single vessel supplying the cord is a persistent left umbilical artery (fig. 7). The arterial arrangement in this monster, however, is not so simple as in the case reported by Schwing, since the original ventral roots of both umbilical arteries have persisted. Duckworth ('07) has also described a case of low-grade symplus dipus (specimen E) with a single umbilical artery. There is good reason, too, for regarding this single vessel as a persistent left artery which takes its origin from the abdominal aorta by means of the primary or ventral root (fig. 9). A more complete consideration of these cases will be given later.

More recently, Langer ('21) described a case of sympodia in which the left umbilical artery was absent and the right appeared as a branch of the right common iliac-hypogastric trunk.

Besides the four cases of sympodia mentioned above which exhibit unilateral persistence of an umbilical artery, there is a

case of symphus dipus described by Gladstone ('06) in which the double arterial supply to the placenta was maintained practically complete. The umbilical artery arose as a single trunk from the abdominal aorta a short distance below the coeliac axis, but soon divided to form a large left and a small right umbilical artery. Neither of these umbilical vessels, however, had any connection with the common iliac-hypogastric trunk.

Single umbilical arteries have also been found associated with other monstrosities than symphodia. Hermann (1822) described two cases of congenital umbilical hernia in which there was a single umbilical artery arising from the aorta. Claudius ('59) reported a case of acephalus in which the umbilical artery appeared as a single branch of the aorta. Strassmann ('95) demonstrated a case of omphalocele in which a single umbilical artery, arising from the left hypogastric, was present. Weil ('97) described a similar fetal defect with the right umbilical artery absent and the left appearing as a branch of the hypogastric. Emrys-Roberts and Paterson ('06) described a case of ectopia viscerum in which the right umbilical artery appeared as a caudal continuation of the abdominal aorta. The left artery was not present.

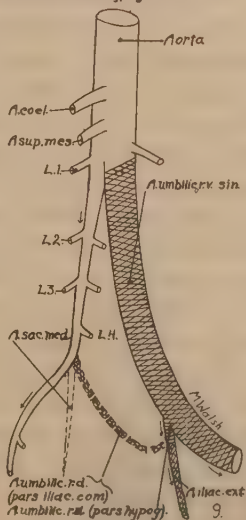
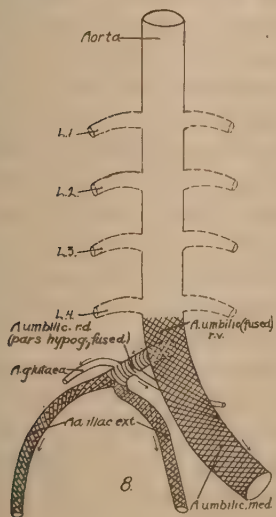
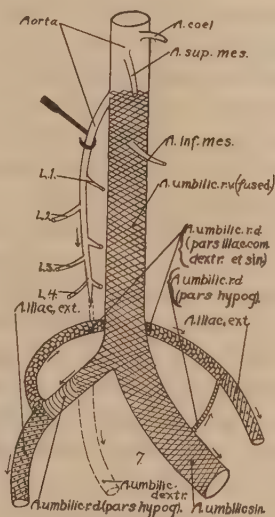
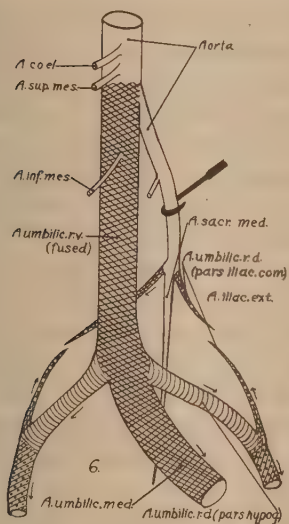
The cases reviewed above furnish, I believe, sufficient evidence to allow us to discount to a considerable extent the emphasis placed by many of the very frequent association of a single and median umbilical artery with the monstrosity symphodia. The formation of a single median artery by the 'fusion' of the original pair can scarcely be regarded as the primary anomaly in symphodia, since occasionally in this type of monster both umbilical arteries may remain almost completely separate, and more fre-

Fig. 6 Diagram suggesting an interpretation of the abdominal arterial system described by Duckworth ('07) for specimen F. (The labeling in this and all succeeding figures is the author's.)

Fig. 7 Diagram suggesting an interpretation of the anomalous abdominal arterial system figured by Odisio ('92).

Fig. 8 Diagram based on Johnston's ('20) description and figure of the arterial supply of a symphodial monster.

Fig. 9 Diagram suggesting an explanation of the anomalous arterial supply figured by Duckworth ('07) for specimen E.



quently only one member of the pair may persist. Furthermore, other types of fetal defects, as omphalocoele, in which the development of the caudal portion of the body is affected, often exhibit similar variations in the arterial supply of the placenta.

While a median umbilical artery is not invariably associated with sympodia, still it is the most common type of variant single umbilical artery found in this class of monster. The development of the median artery appears to be dependent on the persistence of the original ventral roots, whereby the umbilical arteries maintain the same relation to the abdominal aorta as do the vitelline arteries, and undergo the same changes, i.e., are transformed into single vessels. The umbilical arteries are regarded as caudal precocious members of the vitelline series.

The most simple type of median umbilical artery is represented by a combination of the factors 2*a*, 3*a*, and 5*b*, and is the one most commonly encountered in sympodial monsters (Taglicht, '21, et al.). The single artery arises from the abdominal aorta at the lower thoracic or upper lumbar level and passes almost directly to the umbilical cord, having no connections with the common iliac-hypogastric trunk (fig. 4). In these cases the primitive umbilical vessels did not complete the normal caudal migration, no secondary dorsal root connections were established, and the paired vessels were transformed into a single vessel in the same manner as the other paired members of the vitelline series. It is possible, however, that in these cases only one member of the primary pair developed originally, but there is indirect evidence, as already noted, that in many cases two umbilical arteries must have been present at an earlier stage of development. Furthermore, in the case described by Gladstone ('06) the degree of fusion is limited to the short portion adjacent to the aorta. Moorhead ('05) also reported a case (sympus apus) in which the umbilical artery arose from the aorta as a single trunk and entered the cord as a single trunk, but in the intermediate portion it became double for a short distance.

A single umbilical artery having the course and relations of the type under discussion has been interpreted by many (Taglicht, '21, et al.) as a persistent omphalomesenteric artery. In rare



cases (Ballantyne, '98) it seems barely possible that the allantoic circulation may be replaced by the vitelline circulation, but, unless there is sufficient evidence of modification in the placenta to justify such an interpretation, there appears to be no valid ground for advocating it. There is certainly nothing in the ontogenetic history to preclude the interpretation I have offered.

The relations of the single umbilical arteries, in the previous cases where no secondary dorsal connections were made with the aorta, are relatively simple. On the other hand, in cases where the secondary roots were established, followed by either abnormal loss or persistence of either the primary or secondary roots, the relations of the single artery become more complex and it is often difficult to recognize homologies. An additional complication is introduced by the manner of development of the common and external iliac and hypogastric arteries in relation to the dorsal umbilical root. The second case reported in this paper is of this more obscure type, and, in conjunction with my attempt to interpret this anomaly, I wish to discuss rather fully four somewhat similar cases which represent instructive transitional stages in the transformation of a primarily bilaterally symmetrical arterial system into a single median one.

Duckworth ('07) reported a case of *sympus dipus* (?), specimen F, in which the abdominal aorta, below the superior mesenteric artery, divided into a large median ventral and a much smaller dorsal vessel (fig. 6). The ventral vessel appeared at first sight to be the caudal continuation of the abdominal aorta. The dorsal branch, however, was found to be the true aorta and it retained its original dorsal position, continuing caudally upon the vertebral column to end in a middle sacral artery, after giving off distinct branches to the right and left sides of the pelvis. The large ventral trunk arched forwards over the uterine portion of the cloaca and passed downward in the middle line over the rudiment of the bladder. Immediately above the symphysis pubis it gave off symmetrical branches to each side of the pelvis and then bent upwards to enter the umbilical cord as a single vessel. Each of the symmetrical right and left branches, after giving off a femoral branch at the appropriate point, was finally traceable

to the back of the pelvic cavity and came to an end in the close vicinity of the lateral terminal branches of the reduced dorsal aorta.

The condition of the abdominal arterial system in this case is represented by a combination of the factors 2a, 3b, 4b, 5b, 6d, and 8c. The large ventral vessel was produced by the fusion of the primary umbilical arteries which did not complete their caudal migration and retained their original ventral roots. The secondary or dorsal roots were also established, but they underwent considerable atrophy proximal to the point of origin of the external iliac arteries. They were represented in this portion (normally the common iliac portion) by the lateral branches of the dorsal aorta and the dorsolateral branches from the symmetrical right and left branches of the median ventral umbilical artery. These symmetrical branches are homologous with the hypogastric portions of the dorsal umbilical roots. The flow of blood in the latter vessels consequently must be in a direction opposite to that which it takes in the normal arteries. The lumbar portion of the dorsal aorta is also very much reduced in size, due to the diversion of the blood stream brought about by the retention by the umbilical arteries of their primary high origin.

A case similar in many respects to that described by Duckworth ('07) was figured by Odisio ('92). A large ventral artery arose from the aorta below the superior mesenteric artery and continued caudally for a considerable distance as a single vessel (fig. 7). In the region of the pelvis, however, it bifurcated into a small right and a larger left division. The right artery terminated in two relatively large branches; one went back into the pelvis, the other, the external iliac, supplied the right leg. The larger left artery continued practically undiminished in size to the umbilicus, and gave off along its course a small pelvic branch, which in turn gave off the left external iliac artery and then passed dorsally and medially into the pelvis to become continuous with a similar artery from the opposite side. A reduced dorsal aorta was present and it terminated shortly after giving off the lumbar arteries.

A combination of the factors 2a, 4b, 5a, and b, 6b and c, and 8d would produce a result quite similar to this case of Odisio's. The original ventral roots persisted, but failed to migrate caudally the normal distance, and fused for the greater portion of their course, being separate only in the pelvic region. Distal to its union with the right secondary root the right umbilical artery, however, had completely atrophied. The left persisted and became the single vessel of the umbilical cord. Both dorsal umbilical roots were retained, but their early connections with the dorsal aorta were lost, as the latter vessel terminated a short distance cranial to the level from which its dorsal branches originally arose. Although the portion of the abdominal aorta from which the secondary roots arose disappeared, the proximal ends of the roots have remained in continuity. Apparently most of the blood supplied to the left side of the pelvis and left leg must have followed a circuitous route through the vessel of the right side, which is made up of the unfused portion of the right primary umbilical root and the right secondary or dorsal root, reaching the left leg by way of the common iliac portion of the left dorsal root. It is obvious that the small left hypogastric element, of itself, could not supply the larger vessel going to the leg (fig. 7). With the exception of the mistake as to the large ventral artery's being the omphalomesenteric, both Duckworthe and Odisio offered much the same explanations as given above.

In the second case of single umbilical artery described in this paper (figs. 2 and 5) the arterial supply of the abdomen did not differ greatly from the two cases already discussed, and represented a condition such as a combination of factors 2a, 3b, 4c, 5b, 6b, and 8b would produce. The original ventral roots failed to migrate the normal distance caudally, and the primitive umbilical arteries were fused throughout their entire course. Secondary dorsal connections with the aorta were established, but they were subsequently lost proximal to the origin of the external iliac arteries. The portions lost would normally form the common iliac trunks (fig. 5). The distal persisting or hypogastric portions of the dorsal roots were incompletely fused, so that the blood supply of the rudimentary pelvis and 'fused' limbs arose

as a single vessel from the dorsal surface of the umbilical trunk, and later divided into a right and a left branch (fig. 2). From points near the bifurcation of the single trunk small arteries left the hypogastric portions of the right and left branches and passed to the viscera and walls of the shallow pelvis. The main branches continued as external iliac and femoral arteries to the 'fused' lower appendages.

A somewhat different type of single umbilical artery was described by Johnston ('20). The median umbilical artery in this case did not appear as a branch, but as the caudal continuation of the abdominal aorta (fig. 8). "The common iliac arteries were therefore indistinguishable, but the external iliaes arose by a common trunk from the dorsal aspect of the single median artery and almost at once separated, being normal in the remainder of their course so far as could be traced. Their common trunk gave off a few small branches to the rudimentary pelvis and a single gluteal on each side" (p. 211). The arrangement of the abdominal arterial system in this case could be produced by a combination of factors 2*b*, 3*b*, 4*c*, 5*b*, 6*c*, 7 and 8*a*. In contrast with the three cases previously considered, the fused primary umbilical roots have migrated the normal distance caudally. The proximal portions of the secondary roots have atrophied, and along with the fusion of the primary umbilical arteries a fusion of the distal or hypogastric portions of the dorsal roots has also occurred. Because of the loss of the proximal connections of the dorsal roots and the normal lumbar position of the fused primary roots, the lower lumbar and sacral portions of the abdominal aorta have completely disappeared and the single umbilical trunk has assumed secondarily a terminal position.

Another single umbilical artery, having much the same relations as the one described by Johnston ('20), was reported in the same year by Lange, the major difference being that the distal persistent or hypogastric portions of the dorsal umbilical roots did not fuse to form a single trunk. The so-called abdominal aorta accordingly underwent a tripartite division into two lateral vessels supplying the pelvis and legs and a large median artery which turned up and entered the umbilical cord.



The division occurred low in the pelvis some distance caudal to the bifurcation of the inferior vena cava. The proximal ends of the lateral branches of the abdominal aorta, according to my interpretation, are each composed of the hypogastric portion of the dorsal umbilical root and the primitive external iliac artery which grew out from the secondary root. The rôle of the axial or ischiadic artery in the development of the femoral or distal part of these vessels is not taken into account.

In all cases of single median umbilical arteries reviewed there is therefore evidence that the primitive ventral roots have persisted, and it seems probable that this persistence has favored the fusion of the originally paired vessels. Occasionally, however, even in cases where both primary roots are retained one member of the umbilical pair may undergo atrophy distally (Odisio, '92). In a case described by Duckworth ('07), specimen E, to which reference has already been made (p. 331), only the left umbilical artery was present. It arose from the dorsal aorta immediately below the first lumbar arteries and passed caudally to the umbilical cord giving rise to a small gonadic artery and a larger vessel which went to the left leg. The interpretation is suggested in figure 9. The primary umbilical root on the left side persisted and migrated caudally only to a level between the first and second lumbar arteries. The left dorsal umbilical root disappeared proximal to the origin of the external iliac artery and the distal persisting or hypogastric portion linked the external iliac with the left umbilical artery. The history of the right side is more obscure. It is entirely possible that only the left umbilical artery made its appearance originally, otherwise we would have to surmise an atrophy of the primary or ventral umbilical root and a persistence of the secondary or dorsal root—a complete reversal of what occurred on the left side. In the absence of any direct evidence, I prefer the latter interpretation.

In other cases where apparently both secondary umbilical roots were established and the primary roots subsequently atrophied, single arteries are produced by the disappearance distally of one member of the umbilical pair (fig. 3), and the persistent artery appears as a branch of the common iliac-

hypogastric trunk. A somewhat similar condition could also be produced by the failure originally of one member of the umbilical pair to develop. Lateral umbilical arteries of this type have been described in both normal and monstrous fetuses. Schwing ('89) and Langer ('21) reported cases in symphyodial monsters. Weil ('97) found this condition associated with congenital omphalocele. Duckworth ('07) described a persistent left umbilical artery in an abnormal fetus (specimen A). De Archangelo ('01) and Mouchotte ('00) found unilateral persistence of the umbilical arteries in normal fetuses, and the case described in this paper (fig. 1) was found in a normally formed female fetus.

In my specimen (fig. 1) a right lumbar ima was present, and on the same side the umbilical artery was absent. Normally the lumbar ima is more often absent than present (Levy, '02), and, according to Senior ('19), the chief share in the early formation of the dorsal root of the umbilical artery is taken by a vessel which appears as a branch from the fifth lumbar segmental artery. The early atrophy of the distal portion of the right umbilical artery, which presumably occurred in this case, and the consequent diversion of the placental stream to the artery of the opposite side may possibly explain why this fifth lumbar segmental artery was not obliterated during the formation of the right common iliac trunk.

#### SUMMARY AND CONCLUSIONS

The single umbilical arteries described in the literature can be divided into two groups; group 1, including all which arise directly from the abdominal aorta; group 2, those which take origin from the common iliac-hypogastric trunk.

Two cases representative respectively of these two groups are described in this paper. The one belonging in group 1 was found in a symphyodial monster, the other was present in a normally formed female fetus.

Single median umbilical arteries arising from the abdominal aorta are associated only with symphyodia. Occasionally, however, in symphyodia the two umbilical arteries remain almost completely separate. In other cases of symphyodia the distal portion of one

member of the umbilical pair is lost and only one artery is accordingly present in the cord. These exceptions indicate, therefore, that the so-called fusion of the umbilical arteries to form a single median vessel cannot be directly responsible for the monstrous condition.

A list of the several factors which may be concerned in the formation of variant umbilical arteries is given.

The predisposing factor for the formation of single median umbilical arteries, which appear as direct aortic branches, is the persistence of the primary or ventral umbilical roots.

Single umbilical arteries, arising from the abdominal aorta at a high level and passing directly to the umbilicus without any connection with the arterial supply of the lower limbs, have been interpreted by many as persistent omphalomesenteric arteries. These vessels, however, more probably represent fused primary umbilical arteries which did not migrate caudally or become secondarily connected with the aorta at a lower level by means of the so-called dorsal roots. Consequently, such vessels can have no connections with the iliac and hypogastric arteries, which must accordingly develop independently.

Lateral single umbilical arteries which arise from the common iliac-hypogastric trunk have followed the normal plan of development. The absence of an umbilical artery on the opposite side is due either to the atrophy of its distal portion following the establishment of its dorsal connections with the aorta or to the failure of the primary umbilical root to appear originally. In the latter case the dorsolateral vessel leaving the aorta between the fourth and fifth lumbar segments must form the blood supply of half of the pelvis and one leg without any association with the umbilical arterial supply.



## BIBLIOGRAPHY

- BALLANTYNE, J. W. 1898 The occurrence of a non-allantoic or vitelline placenta in the human subject. *Trans. Edinb. Obstet. Soc.*, vol. 23, pp. 54-81, or *Scott. Med. and Surg. Jour.*, vol. 2, pp. 296-311; 385-394.  
1902-04 *Manual of ante-natal pathology and hygiene*. 2 vols. Edinburg.
- CLAUDIUS 1859 *Die Entwicklung der herzlosen Missgeburten*. Kiel.
- DAWSON, A. B. 1922 Some significant features of the anatomy of a symelian monster. *Proc. Amer. Assoc. Anat., Anat. Rec.*, vol. 23, p. 15.
- DAWSON, A. B., AND REIS, J. H. 1922 An anomalous arterial supply to suprarenal, kidney, and ovary. *Anat. Rec.*, vol. 23, pp. 161-167.
- DE ARCHANGELO, E. 1901 Sull'arteria ombelicale unica nel feto umano normale. *Arch. di Ostet e Ginec., Napoli, Ann.* 8, p. 419.
- DUCKWORTH, W. L. H. 1907 A critical description of three cases of single hypogastric artery in the human fetus. *Proc. Cambridge Philos. Soc.*, vol. 14, p. 325.
- EMRYS-ROBERTS, E., AND PATERSON, A. M. 1906 A case of ectopia viscerum, associated with spina bifida and other abnormalities. *Jour. Anat. Physiol.*, vol. 40, pp. 332-356.
- FELIX, W. 1910 Zur Entwicklungsgeschichte der Rumpfarterien des menschlichen Embryo. *Morph. Jahrb.*, Bd. 41, Heft 4, S. 577.
- GLADSTONE, R. J. 1906 A symelian monster (*Sympus dipus*). *Brit. Med. Jour.*, vol. 2, p. 1704.
- HERMANN 1822 *Medicin. chirurg. Zeitung, Innsbruck*. (Cited by Wolff 1899.)
- HOCHSTETTER, F. 1890 Ueber die ursprüngliche Hauptschlagader der hinteren Gliedmasse des Menschen und der Säugetiere, nebst Bemerkungen über die Entwicklung der aorta abdominalis. *Morph. Jahrb.*, Bd. 16, S. 300-318.
- JOHNSTON, T. B. 1920 The anatomy of a symelian monster. *Jour. Anat.*, vol. 54, pp. 208-216.
- LANGE, E. 1920 Ueber eine Sirenenmissbildungen insbesondere das urogenital System der Sirenen. *Stud. z. Path. d. Entwickl.*, Bd. 2, S. 467-526.
- LANGER, E. 1921 Über Sirenenbildung. *Zeitschf. f. Geburtsch u. Gynäk.*, Bd. 84, S. 131-158.
- LEVY, G. 1902 Morphologia delle arteriae iliache, Parte 2. *Archiv. Ital. di Anat. e di Embriol.*, V. 295.
- McMURRICH, J. P. 1920 *The development of the human body*, 6th ed. Philadelphia.
- MOORHEAD, G. 1905 The anatomy of a sirenomelian monster. *Jour. Anat. Physiol.*, vol. 39, pp. 450-561.
- MOUCHOTTE, J. 1900 Artère ombilicale unique. *Bull. et Memoires de la Soc. Anat. de Paris.* 75 An., 6e serie, T. 2, pp. 786-788.
- ODISIO, L. 1892 Studio anatomico ed istologico sopra un sirenomele. *Giorn. della R. Accad. di Medicina di Torino, Anno* 55, vol. 40.



- PIERSOL, G. A. 1907 Human anatomy. Philadelphia and London.
- SCHWING 1889 Eine Sirenenbildung bei einen Zwillingskinde. Zentralbl. f. Gynäk., Bd. 13, S. 484-485.
- SENIOR, H. D. 1919 The development of the arteries of the human lower extremity. Am. Jour. Anat., vol. 25, pp. 55-95.
- STRASSMAN, P. 1895 Missbildung mit grossen Bauchbruch. Fehlen der Nabelschnur, Prolaps der Placenta. Zeitschr. f. Geburtsh. u. Gynäk., Bd. 31.
- TAGLICH, F. 1921 Ein Fall von Sirenenmissbildung mit cystischer Sakralgeschwulst. Arch. f. Path. Anat., Bd. 230, S. 525-563.
- TANDLER, J. 1903 Zur Entwicklungsgeschichte der menschlichen Darmarterien. Anat. Heft, Bd. 23, S. 187.
- WEIL, E. 1897 Omphalocele congénitale—Anomalies multiples et arrêts de développement. Bull. Soc. Anat., 5e ser., T. 11, pp. 121-123.
- WOLFF, B. 1899 Über Missbildungen mit einfacher Nebelarterie. Arch. f. Gynäk., Bd. 57, Heft III, S. 635-661.

